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Thermal and Spatial Ecology of Three Species of Water Snakes (Nerodia) in a Louisiana Swamp.

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THERMAL AND SPATIAL ECOLOGY OF THREE SPECIES OF WATER SNAKES (NERODIA) IN A LOUISIANA SWAMP.

A Dissertation

Submitted to the Graduate Faculty of the
Louisiana State University and
Agricultural and Mechanical College
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in

The Department of Zoology and Physiology

by
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Thomas Claud Michot

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ABSTRACT

Biotelemetry was used to study thermal and spatial relationships in Nerodia fasciata confluens, N. c. cyclopion, and N. r. rhombifera. Twenty snakes were monitored between April 1978 and September 1979 in Ascension Parish, Louisiana. Laboratory-determined preferred temperature ranges were compared to environmental temperatures from air, soil, and water to predict thermally optimum microhabitats. Comparison of observed and predicted microhabitats for each observation showed that N. fasciata was found more frequently in the thermally optimum microhabitat than were N. cyclopion and N. rhombifera. Nerodia cyclopion consistently showed thermal nonconformity by altering the relationship between body (BT) and ambient (AT) temperatures so that BT was closer to the preferred range when AT was high or low. All species showed the highest degree of thermoregulation in spring/fall; the lowest degree of thermoregulation was found in summer for N. cyclopion, and in winter for the other two species. Snake movements showed a high degree of variation. Snakes typically stayed in a home area for about 20 days before making a major movement (>100 m). Nerodia fasciata moved significantly more than N. rhombifera. The latter species stayed closer to land, spent more time underground, and, when in water, was found at greater depths than the other two species. The mean home range polygon for all observations was 5.96 ha, with values ranging from 0.03 to

15.39 ha. Home range size showed much variation and was not significantly correlated with species, sex, reproductive condition, weight, time of year, length of tracking period or interval between observations.

INTRODUCTION

The body temperature of an animal can have an important effect on its performance in nature. Significant insight into the thermal ecology of free-ranging animals is gained by the use of temperature-sensitive radiotelemetry systems. The use of telemetry allows aquisition of data from snakes which need not be visible and creates only a minimum of disturbance to the animal. This study investigates the extent to which temperature influences microhabitat use in water snakes and evaluates deep body temperature in the field with respect to ambient temperatures and to the preferred temperature of each species. In addition, movements and home ranges were studied to determine factors affecting spatial relationships.

Most physiological processes are temperature-dependent. This dependence is based at the molecular level since there is a single temperature at which each enzyme has an optimal activity (Hainsworth and Wolf 1978). Consequently the rate of biochemical reactions, and hence the functioning of organs, organ systems, and whole organisms, is affected by temperature. In endotherms all physiological functions are performed at the same temperature, which is maintained primarily by metabolic heat production and regulation of heat flow. Although ectotherms can operate over a broader range of body temperatures, each species is believed to have a specific temperature or temperature range at which the physiological processes are optimal (Dawson 1975).

The preferred temperature, or thermal preferendum, is operationally defined as the temperature range on a thermal gradient in which congregation occurs, or in which the most time is spent (Reynolds and Casterlin 1979). Although the preferred temperature can vary due to prior thermal acclimation (constant temperature exposure over a period of time), the "final preferendum" is essentially independent of prior thermal experience because it is the temperature at which preference and acclimation are equal (Fry 1947). The final preferendum is believed to be genetically controlled, while acclimation is a nongenetic physiological adaptation (Prosser 1973).

Many reptiles have shown a tendency to regulate their body temperature to some extent; in fact, species which show no attempt to thermoregulate are rare (Heatwole 1976). Most field studies on thermal ecology of reptiles have dealt with lizards, especially desert thermophiles that are active at body temperatures above 36 C (Bartholomew and Tucker 1963, Bartholomew et al. 1965, Bowker and Johnson 1980, Crawford 1972, DeWitt 1967, Georges 1979, Hammel et al. 1967, Huey and Pianka 1977, Heatwole 1970, Huey and Slatkin 1976, Huey and Webster 1976, Licht et al. 1966, Muth 1977, Parker and Pianka 1975, Patterson and Davies 1978, Pianka 1971, Ruibal and Philibosean 1970, Schall 1977, Vance 1973, and others). Snake field studies have dealt with desert species (Hammerson 1977, 1979, Hirth and King 1969, Moore 1978), tropical pythons (Hutchison et al. 1966, Johnson 1972, 1973, Van

Mierop and Barnard 1978) and some temperate species, mostly Thamnophis (Carpenter 1956, Aleksiuk and Stewart 1971, Fleharty 1967, Gregory and McIntosh 1980, Hart 1979, Stewart 1965, Vincent 1975). Osgood (1970) studied the effect of temperature on embryological development in water snakes. Mushinsky et al. (1980) indicated that temperature may be an important factor in the behavioral ecology of water snakes.

The species I studied were Nerodia cyclopion cyclopion (green water snake), N. fasciata confluens (broad-banded water snake), and N. rhombifera rhombifera (diamond-backed water snake). These three species made up 86% of a six-species water snake guild in a Louisiana swamp (Mushinsky et al. 1980). Previous studies of this snake guild have dealt with the ecological relationships of these species with reference to the resources of time (Mushinsky and Hebrard 1977a), food (Mushinsky and Hebrard 1977b), space (Hebrard and Mushinsky 1978) and temperature (Mushinsky et al. 1980). These reports provide a broad framework for a detailed investigation of the thermal and spatial ecology of the three most abundant species.

MATERIALS AND METHODS

STUDY AREA

The study area, Bluff Swamp, is located 21 km south of Baton Rouge, Louisiana, near the northern end of the Pontchartrain Basin in Ascension and Iberville parishes. The 2650 ha area consists of cypress-tupelo swamp and bottomland hardwood forest types. Bayou Braud and Alligator Bayou are the two main waterways in the study area, and they flow north through two control gates into Bayou Manchac, a former distributary of the Mississippi River. Local rainfall supplies water to the swamp, and water level in Alligator Bayou fluctuated within the range of 60 to 270 cm above mean sea level during the study, April 1978 to September 1979.

DATA COLLECTION

Snakes were transported to the laboratory for transmitter implantation. Species, sex, reproductive condition, snout-vent length, and weight were recorded. Subcaudal scales were clipped to correspond to individual identification numbers. A snake was temporarily cooled until relatively immobile to facilitate transmitter implantation. A lateral incision was made between two ventral scutes in the posterior third of the body, and a transmitter was inserted into the coelom. After the cut was sutured, the snake was placed in an outdoor recovery pen where it was subject to ambient temperature and photoperiod regimes.

The radiotelemetry transmitter was a model-L Mini-mitter (Indianapolis, Indiana) coated with a paraffin compound. The cylindrical transmitter packages varied in length from 2.5 to 5.0 cm and in weight from 10.7 to 24.0 g, depending on battery size. The smaller transmitter packages were used in smaller snakes. The transmitters were temperature sensitive; thus the body temperature of the snake could be determined by the rate of the signal, which increased with increasing temperatures. Each transmitter was calibrated as specified by the manufacturer, who claimed an accuracy of $\pm$ 0.2 C. The receiver was a crystaltuned six channel converted walkietalkie (Lafayette model HA420). A rectangular, aluminum antenna was used for directionality. Reception distance varied, but was usually about 100 m.

Twenty snakes were used. Eight were gravid females, six were nongravid females, and six were males. Since previous studies (Mushinsky et al. 1980) suggested that Nerodia cyclopion is a more active thermoregulator than the other two species, my study concentrated on this species. Sex and size data on the individuals used in this study are presented in Table 1. Analyses of variance in the results section were constructed so as to minimize the effect of biases stemming from unequal samples. I am assuming that behavioral differences between individuals could be explained by species, sex, size, or reproductive state differences.

The telemetered snakes were released at the capture site, usually three to five days after capture. Observations were made periodically from one hour after release until the snake was lost, died, or was recaptured. The snakes were divided into two categories based on the interval between observations. The spotcheck approach was used from April 1978 through February 1979; this approach involved locating snakes every two to three days and making one to four observations in a given day. The continuous monitoring approach involved taking readings every 30-40 minutes for a period of 24 hours and was used from March through September 1979.

Values for approximately 25 variables were recorded at each observation. Temperature data included body temperature (recorded as signal frequency in beats per minute), air

Table 1. Sex and size characteristics of snakes used in telemetry study.

Species	N	Sex[a]			Snout-vent[b]		Weight[c]	
		M	G	N	Mean	Range	Mean	Range
cyclopion	11	3	6	2	72	58- 89	346	134- 607
fasciata	4	-	1	3	72	65- 75	274	207- 337
rhombifera	5	3	1	1	90	72-106	583	311-1036
Total	20	6	8	6	76	58-106	391	134-1036

[a] M=male, G=gravid female, N=nongravid female

[b] Length, in centimeters

[c] In grams

temperature (in the shade, 30 cm above the surface), sun temperature (probe lying flat on a wooden substrate in full sun for three minutes), water temperature on the surface (at a depth of five centimeters) and on the bottom (three meters maximum), and substrate or soil temperature, if applicable. The temperature that was thought to have the greatest effect on the snake's body was designated as the ambient temperature (AT). If the snake was in air, the shade temperature was used as AT, and the portion of the body exposed to sunlight (vs. shaded) was recorded. A telethermometer (Yellow Springs Instruments model 42SC) with a fastreading (7.0 sec) probe on a 3 m lead was used for all temperature readings.

Other variables associated with each observation included time (CST), cloud cover, whether or not the sun was visible, whether or not the snake was observed visually, the snake's behavior, distance of the snake from the land/water interface, water depth, microhabitat (air, water, or soil), height above substrate, distance moved, and compass bearing from last site.

DATA ANALYSIS

THERMAL ECOLOGY

The Effect of Temperature on Choice of Microhabitat

Sources of variation in thermal microhabitat optimization

To investigate the effect of temperature on variation in microhabitat use, I developed a model that would predict, for each observation, the optimal microhabitat for an individual of a given species based on its preferred temperature range. A correlation between predicted and observed microhabitats was then obtained, and this correlation was regressed against different class variables in an analysis of variance.

The preferred tempereture ranges used in the model were obtained from a laboratory study by Walley and Mushinsky (in press), who used specimens from the same locality as the present study; the two studies were conducted concurrently. A number of assumptions was inherent in my choice of a preferred temperature range. One assumption is that preferred temperatures obtained from a thermal gradient are more indicative of innate preference than field (eccritic) temperatures, which may be biased by heating and cooling phases and possible unavailability of preferred temperatures (Heatwole 1976).

The preferred temperature range consisted of values between the mean preferred temperature (MPT) minus one standard deviation and the MPT plus one standard deviation. The ranges used in this study are presented in Table 2. An assumption is that each species has its own preferred range, which does not vary seasonally or diurnally (see Heinrich 1977). DeWitt and Friedman (1979) suggested that, since most body temperature (BT) distributions are negatively skewed, the median plus or minus 34% would be a better estimate of preferred temperature range than the mean $\pm$ 1 SD. The results of Walley and Mushinsky (in press), however, show that one species (Nerodia fasciata) did not exhibit a negatively skewed BT distribution and that the degree of skewness in the other two was so slight that the difference between the mean and median was less than 0.3 C. Thus I used mean and standard deviation to define the preferred temperature range; these parameters were also used by Magnuson et al. (1979) to define the fundamental thermal niche.

The program for the microhabitat prediction model is presented in Appendix 1. The various environmental temperatures available to the snake at the exact place and time of the observation were used as input for the model, and the predicted microhabitat was that which was thermally optimum to the snake. A maximum of six temperatures from three microhabitats was available at any given time: air (shade, sun, and substrate), water

Table 2. Thermal statistics of three species of water snakes in a gradient (after Walley and Mushinsky, in press).

Species	N	MBT[a]	SE	Range	Preferred Range[b]
cyclopion	253	25.16	0.20	15.1-35.1	21.90-28.42
fasciata	230	27.12	0.23	20.7-38.9	23.64-30.60
rhombifera	250	27.29	0.24	15.3-37.2	23.54-31.04

[a]MBT=mean body temperature in degrees celsius.

[b]Preferred Range=MBT $\pm$ 1 s. d.

(surface and deep), and soil (subsurface). If only one microhabitat had a temperature within the preferred range, that microhabitat was the predicted microhabitat. If all temperatures were below or above the preferred range, then the microhabitat with the highest or lowest temperature, respectively, was designated as the predicted microhabitat. This designation is based on the assumption that an animal tends to increase heat loads when ambient temperatures are low, and reduce heat loads when ambient temperatures are high (Huey and Pianka 1977). Observations in which two or three microhabitats had temperatures in the preferred range did not have a single predicted microhabitat, but were treated separately.

A new variable, TMO (thermal microhabitat optimization), was generated to represent a measure of behavioral thermoregulation. The value of TMO was 1 if the predicted microhabitat equaled the observed microhabitat, and 0 if the two were not equal. If two microhabitats had temperatures in the preferred range, then TMO was 1 if the snake was observed in either one of those two microhabitats, and 0 if not. Those observations in which all three microhabitats were in the preferred range had a TMO of 1, since the snake would be in an optimum ambient temperature regardless of microhabitat. Thus a snake was in a thermally optimal microhabitat if TMO=1, and this value presumably represents behavioral thermoregulation. The mean TMO (with a value from zero to one) for a given group of observations, then,

represents the proportion of observations in which the snakes were thermoregulating.

To investigate differences in thermoregulation between certain groups of observations, an analysis of variance was run on the dependent variable TMO with 10 independent variables as possible sources of variation. The weight class was designated as HEAVY if the snake's body weight was greater than 391 g (the mean for all snakes tested), and LIGHT if less than 391 g. The light condition was designated as DAY if the observation was made between sunrise and sunset, and NIGHT otherwise. Observations made in March, April, May, September or October were combined into the season of SPRING/FALL; SUMMER included June through August, and WINTER was November through February. Significance levels were based on the Type IV sums of square adjusted for unbalanced data.

Further insight into the variation in thermoregulation was obtained by comparing the mean TMO of the different levels within each class variable. The least squares mean (LS mean) was used rather than the arithmetic mean since the former is adjusted for unbalanced sampling which could confound inferences based on the latter. Student's t-test was used to test the null hypothesis that LS mean$_i$=LS mean$_j$ for all appropriate combinations within each source category. The null hypothesis was rejected when $P>0.05$.

Since it has been suggested (McNab and Auffenberg 1976, Patterson and Davies 1978, Osgood 1970, Hirth and King 1969, and others) that body temperature and temperature preference are correlated with sex, body size, and reproductive condition, these variables, as well as sampling method, are included in the ANOVA to assess their significance in thermoregulation. It is also important that interpretation of the effects of other variables not be confounded by data that are unbalanced with respect to these four variables.

Differences in the number of snakes sampled in air, water, or soil do not bias the mean TMO because the value of microhabitat as a function of snake behavior was included in the model and hence determined the value of TMO for each observation. It would be erroneous, then, to adjust the means of other independent variables for data that do not have an equal number of samples in each microhabitat. For this reason microhabitat could not be included as an independent variable in the above ANOVA. Instead, another analysis of variance was run which included the seven class variables used above in addition to microhabitat as a main effect and its interactions with species, season, and light.

Thermal microhabitat optimization versus microhabitat use patterns

A high frequency of observations in a given microhabitat is expected when behavioral regulation is high.

Conversely, when the mean TMO for a microhabitat is low, a low occurrence is expected. The validity of these predictions can be tested by comparing observed microhabitat frequencies within the variables light, season, and species with the above patterns of behavioral thermoregulation.

Body Temperature Variation

Relationship between body temperature and ambient temperature

A perfect thermoconformer, that is an animal whose body temperature (BT) is always equal to ambient temperature (AT), must depend on behavioral thermoregulation to regulate BT. On the other hand, if an animal can maintain some control over BT relative to AT, less behavioral thermoregulation may be required. In this section the relationship between body temperature and ambient temperature, and its variation among groups, are examined.

Huey and Slatkin (1976) pointed out that the slope of regressing BT on AT equals 1 for a perfect thermoconformer (BT=AT), and 0 for a perfect thermoregulator. This type of thermoregulation is referred to as thermal nonconformity, without specifying whether it is physiological or behavioral. Crawshaw (1979) cautioned against implying physiological control without implicating a thermally sensitive regulatory system and showed that passive vasomotor changes could have a thermoregulatory effect.

The variable TX represents the difference between BT and AT for each observation (TX=BT-AT). Thus the value of TX would be zero if BT=AT, greater than zero if BT>AT, and less than zero if BT<AT. The value of TX would be relevant in terms of the animal's preferred temperature range, or thermal preferendum. If AT is within the preferred range, then there would be no need to maintain a gradient between BT and AT (TX=0). When the ambient temperature is above the preferred range, a thermal nonconformer would attempt to keep a cooler BT (TX<0), and when AT is below the preferred range, BT would be kept warmer (TX>0).

Again using the thermal preferenda (see Table 2) established by Walley and Mushinsky (in press), I assigned each observation to one of three temperature classes: HIGH (AT > maximum preferred temperature), MID (AT in preferred range), or LOW (AT < minimum preferred temperature). Thermal nonconformity would be indicated in a group of observations whose mean TX was negative and significantly different from zero when temperature class (TEMPCL) = HIGH, positive and significantly different from zero when TEMPCL = LOW, and not significantly different from zero when TEMPCL = MID. An analysis of variance was run on the dependent variable TX, with the independent variables weight class, sex, reproductive condition, sampling method, species, temperature class, season, light, and the species x temperature class interaction.

Interaction between thermal nonconformity and thermal microhabitat optimization

Seasonal and diel variation in microhabitat use patterns were looked at within species to see if they were consistent with patterns of thermal nonconformity and microhabitat optimization. This required subdividing the data into blocks with potentially small or missing samples, so only the unadjusted arithmetic means could be used. For each level of species x season the mean TX and TMO for the interaction of light x microhabitat x TEMPCL was considered. A t-test on each mean tested the null hypothesis that the mean was equal to zero. Thermal nonconformity was indicated when the mean TX was significantly ($P<0.05$) different from zero in the direction of the preferred temperature. Behavioral thermoregulation was indicated if the TMO mean was not significantly different from one (using mean $\pm$ 2 SE as 95% confidence limits).

Solar effects

To investigate the effect of solar radiation on the relationship between BT and AT, the mean TX for snakes observed in air in the LOW temperature class was compared among three solar conditions: night, day with visible sun, and day with no visible sun. If visible solar radiation was being used to raise body temperatures, the mean TX would be significantly greater than zero only when the sun was

visible. If visible and invisible solar radiation were being used, the mean TX for nocturnal observations would not be significantly different from zero whereas the other two means would indicate thermal nonconformity. No solar effect would be indicated if the three means were not significantly different.

Whenever a snake in air was seen, the percentage of the body that was exposed to sunlight, as opposed to shade, was recorded. These values were regressed against the corresponding TX values to test for correlation between TX and percent sun.

Time effects

In the previous analyses I viewed each observation as a separate entity, not considering that many may be linked on the time axis. The environmental temperatures available to a snake vary in both space and time, and one of the advantages of radiotelemetry is that the various biological parameters associated with an individual can be monitored over a period of time.

Body temperature variation over time. Pairs of observations on the same snake that were less than 24 h apart ($\bar{x}$ interval = 2.0 h) were used to investigate the relationship between time and body temperature variation. For each pair, i and i+1, I considered body temperature (BT_i and BT_{i+1}), ambient temperature (AT_i and AT_{i+1}), and whether or not the snake changed microhabitats between i and i+1. To simplify

analysis BT and AT were put into temperature classes (HIGH, MID, or LOW) relative to each species' preferred temperature range.

Thermoregulatory categories. If thermoregulation can be considered as a type of goal-oriented behavior, then the goal of a thermoregulating snake would be to keep its body temperature in the MID range. In keeping with this assumption, I assigned each of the different "pathways" by which a snake reached BT_{i+1} to one of three thermoregulatory categories. If BT_{i+1} was not in the MID class, then the category was designated as nonthermoregulator. This category includes snakes whose BT moved out of the MID range from i to i+1.

Those snakes with BT_{i+1} in the MID range, but whose BT was always in the same class as AT, were designated as thermoconformers. These snakes may well be, and probably are, behaviorally thermoregulating by staying in or moving to a microhabitat in the MID temperature class (thermal microhabitat optimization). Also included in the thermoconformer category are those snakes who started out with AT_i and BT_i in HIGH or LOW and did not change microhabitat, but the ambient temperature warmed or cooled over time into the MID range, and BT followed suit. This category may also include those individuals that changed microhabitats to one in the MID range, and the BT changed as a result (the effect of microhabitat change will be considered separately below).

The third thermoregulatory category is thermal nonconformer. Such animals used a gradient between BT and AT (TX) for thermal gain, and could change the gradient when appropriate. In the first and/or the second observation AT was in HIGH or LOW while BT was in MID. In other words, body temperature behaved independently from ambient, and ended up in the MID range. A microhabitat change may or may not have occurred between i and i+1. An assumption in this model is that temperatures within the same class have equal weights, i.e., MID is thermally optimal and HIGH and LOW are not optimal.

Effect of microhabitat change. Snakes achieve thermoregulation by being in a microhabitat in the MID range, by altering the relationship between BT and AT, or by moving from an unfavorable to a thermally favorable microhabitat. This latter behavior has been termed thermokinesis by Fraenkel and Gunn (1961) and can be used in conjunction with thermoconformity or thermal nonconformity. It is difficult to determine whether a change in BT was the direct result of a microhabitat change, for the changes in two ambient temperatures from i to i+1 must be considered. In some cases microhabitat_i was in the same temperature class as $\text{microhabitat}_{i+1}$, and sometimes a change was made to a microhabitat in a less favorable temperature class. A change in microhabitat was designated as thermokinesis only if AT_i was not in MID, and AT_{i+1} was in MID, or if the

temperature of microhabitat$_i$ moved out of the MID range and the animal changed into microhabitat$_{i+1}$, which was in MID.

Eccritic body temperatures

The mean body temperature (MBT) of reptiles in the field is called the eccritic temperature (Heatwole 1976). The eccritic temperatures for each species were tested for interspecific, seasonal, and diel variation by t-tests, and were compared with preferred (laboratory) temperatures.

SPATIAL ECOLOGY

Land/Water Relations

An important factor in the use of available habitat by water snakes is alteration of the existing shoreline (land/water interface) due to water level fluctuations. Water level on the study area was influenced by local rainfall as well as by man-operated control structures, and fluctuations were sometimes of considerable amplitude. As a result, a given geographical point could be on dry land and 300 m from the nearest water at one time of year, and be inundated and 300 m from land at another time.

At each observation I recorded the distance (in meters) from the nearest land/water interface; the value was positive if the snake was in water, and negative if on land. Thus it could be said that snakes in a certain class level were found at the land/water interface when the mean distance was not significantly different from zero; if, however, the t-test showed that the mean was significantly different from zero, then the animals were in open water (positive mean) or on dry land (negative mean). "Open" water here only indicates distance from land, not absence of trees or vegetation. An analysis of variance was used to obtain least squares (unbiased) means so that results

would not be confounded by differences in sample size. This is especially important in that water level was included as an independent variable so that significance levels were independent of sample size bias by water level. The water level was designated as HIGH when the water was greater than 1.5 m (5 ft) above mean sea level, and LOW if less than 1.5 m. Above 1.5 m the backswamp was inundated and below this level the water was confined for the most part to established waterways and permanent bodies of water.

In addition to the above analysis, an ANOVA was run on the dependent variable DEPTH (measured in centimeters) for snakes that were observed in water. The results of these two analyses are presented simultaneously, since both are pertinent to land/water relations. The independent variables were the same for both models: weight class, sex, reproductive condition, species, season, water level, light, species x season, species x water level, species x light, season x light, water level x light, and species x season x light. The effects of these variables are shown by differences in LS means. T-tests were used to test the null hypothesis that the LS mean distance from land/water interface is equal to zero, and the null hypothesis that LS mean depth for $level_i$ is equal to that for $level_j$ within each source.

Linear Movement Patterns

Movement rates

In this section only the distance moved between points is considered, and not the direction of movement; hence observations are considered as points on a line (the next section will consider observations as points on a plane). Though I attempted to standardize the intervals between observations, locating the snakes was not always as predictable as desired, so there is considerable variation in this parameter. To compensate, a movement rate (meters/day) was used in the analyses. For multiple observations within the same day, movements were summed until an interval of at least 24 h was reached, and the total was considered as one observation. When the interval between observations was greater than one day, the distance was divided by the interval to obtain a meters/day value. This figure, then, would be a minimum estimate, since the assumption is that the animal moved in a straight line from one point to the next; in reality, additional movements may have occurred between observations.

A log transformation was used to obtain a normally distributed variable that could be analysed by parametric statistical methods. An analysis of variance was run with the log of distance moved per day as the dependent variable. Independent variables included the

main effects of species, sex, reproductive condition, season, weight class, and water level, as well as the interactions of species x season, species x water level, and season x water level.

In addition to the above discrete variables, I examined several continuous variables which reflect environmental conditions (photoperiod, temperature, and water level) that could have influenced movements. These three environmental parameters were represented by eight sources of variation (independent variables) in an analysis of variance with the log of distance moved per day as the dependent variable. Photoperiod is simply represented by the hours of daylight on the day of observation. Temperature is represented by the mean of the maximum and minimum temperatures between observations ($=T_{max}+T_{min}/2$), the range between these values ($=T_{max}-T_{min}$), and the interaction between mean and range. Water level is represented by the level (above mean sea level) at the time of observation and the change in water level between observations. The distance from the land/water interface at the time of observation was included, as well as the change in this value between observations; these are not necessarily dependent on water level, but may be influenced by the behavior of the snakes.

Daily activity

Observations less than 12 h apart ($\bar{x}$=1.31 h) were used to analyse daily activity patterns. A snake was considered to be active when a detectable linear movement occurred and inactive when there was no movement between observations.

Planar Movement Patterns

Home range

This section deals with snake movements in two-dimensional space, including temporal considerations where possible. The generally accepted definition of home range is that given by Burt (1943, p. 346), who stated that it is the "area normally traversed by an individual animal or group of animals during activities associated with feeding, resting, reproduction, and shelter seeking." I am assuming that all observations for a given individual fall within its home range. The method most often used to calculate home range (Harestad and Bunnell 1979) is the minimum area method of Hayne (1949), in which the outermost points are connected so as to form the smallest possible convex polygon. Koeppl et al. (1975) calculated home range as the area of a standard ellipse whose center was the mean of the x and y coordinates of all points, and whose principle and minor axes were

equal to two times the standard deviations of x and y ($A=pi \cdot s_x \cdot s_y$). Both elliptical and polygonal methods were used to calculate home ranges of individuals monitored for more than 10 days.

Movements within home range

To analyse movement patterns within the home range I used the concept of "home areas" (Warden and Lorio 1975). A home area consisted of two or more points within a home range that were less than 100 m apart and spanned a time period of at least two days (my criteria). A movement to a point greater than 100 m from the previous point or group of points was termed a "major movement."

RESULTS

THERMAL ECOLOGY

THE EFFECT OF TEMPERATURE ON CHOICE OF MICROHABITAT

Sources of Variation in Thermal Microhabitat Optimization

The overall mean TMO for all observations was 0.67, indicating that these water snakes were behaviorally thermoregulating in 67% of the observations. Results of the ANOVA (Table 3) show that the population means for the 11 sources of variation are not equal ($F=10.68$, $P=0.0001$). A significant ($P<0.05$) amount of variation in the model was due to the main effects of weight class, species, and season, as well as the interactions species x season, light x season and species x light x season.

When species is considered as a main effect (Table 4), Nerodia fasciata showed significantly higher behavioral thermoregulation than either N. cyclopion or N. rhombifera, but the difference between the latter two species is not significant. Interspecific differences within seasons were significant only between N. fasciata and N. rhombifera in spring/fall, and no winter differences were significant (Table 5). In the summer, N. fasciata showed a significantly higher TMO than N. rhombifera, and that of N. cyclopion was significantly lower than either of the others. N. cyclopion never showed an LS mean that was significantly higher than either of its congeners.

Table 3. Analysis of variance in thermal microhabitat optimization (TMO) for three species of Nerodia.

Source	DF[a]	SS[b]	MS[c]	F[d]	PR>F[e]
Model	21	36.9340	1.7588	10.68	0.0001
Error	570	93.8346	0.1646		
Corrected Total	591	130.7686			
Weight Class	1	3.4417		20.91	0.0001
Reproductive Condition	1	0.1880		1.14	0.2856
Sex	1	0.5749		3.49	0.0622
Sampling Method	1	0.2395		1.45	0.2283
Species	2	1.4742		4.48	0.0118
Light	1	0.2838		1.72	0.1897
Season	2	4.0170		12.20	0.0001
Species x Light	2	0.0793		0.24	0.7859
Species x Season	4	7.3860		11.22	0.0001
Light x Season	2	1.1043		3.35	0.0356
Species x Light x Season	4	1.9924		3.03	0.0174

[a] Degrees of Freedom

[b] Sums of Squares

[c] Mean Squares

[d] F-statistic

[e] Probability of erroneously rejecting the null hypothesis

Table 4. Least Squares mean thermal microhabitat optimization (TMO) values for water snakes by species, light, and season.

Class	Level	N	LSmeans	SE	Significance[a]
Species	*cyclopion*	304	0.69	0.06	A
	fasciata	153	1.00	0.11	B
	rhombifera	135	0.76	0.05	A
Light	Day	447	0.86	0.05	A
	Night	145	0.78	0.07	A
Season	Spring/ Fall	201	1.02	0.06	A
	Summer	352	0.82	0.05	B
	Winter	39	0.62	0.09	C

[a] LS means in each class with the same letter are not significantly different ($P>0.05$).

Table 5. TMO values (LS mean ± SE (N)) for species x season interactions of water snakes.

Species	Season			
	Spring/Fall	Summer	Winter	Signif[a]
cyclopion	0.97 ± 0.07 (84)	0.39 ± 0.04 (210)	0.72 ± 0.16 (10)	ABA
fasciata	1.21 ± 0.13 (73)	1.20 ± 0.10 (69)	0.59 ± 0.11 (11)	AAB
rhombifera	0.88 ± 0.07 (44)	0.88 ± 0.07 (73)	0.54 ± 0.18 (18)	AAB
Signif[a]	AAB	ABC	AAA	

[a] LS means within each class with the same letter are not significantly different (P>0.05).

Differences in behavioral thermoregulation between seasons (Table 4) were significant for all three combinations, with the highest regulation occurring in spring/fall and the lowest in winter. Seasonal variation within species (Table 5) showed some differences. Nerodia cyclopion had its lowest regulation in the summer (39%), which was significantly lower than spring/fall (97%) or winter (72%), but no significant difference was found between the latter two seasons. N. fasciata and N. rhombifera, on the other hand, showed the least thermoregulation in the winter; LS means for spring/fall and summer were significantly higher than for winter, but they were not different from each other.

Diurnal variation in TMO was significant neither as a main effect (Table 4) nor within species. The only significant difference between day and night behavioral thermoregulation was in the summer when snakes observed in the day were in a thermally optimum microhabitat 92% of the time as opposed to 72% at night. This summer condition is most pronounced in Nerodia cyclopion, which was behaviorally thermoregulating in 53% of the day observations but in only 24% at night (Table 6). N. rhombifera also showed significant diel variation in the summer with 100% TMO during the day and 72% at night. Nerodia fasciata seemed always to be in the optimum microhabitat day and night with the exception of winter night.

Snakes in air generally exhibited a significantly higher degree of thermal microhabitat optimization than

Table 6. TMO LS means for the interaction of species x season x light for three species of water snakes.

Species	Season	Light	N	LS mean	SE	Signif[a]
cyclopion	Spring/Fall	Day	72	0.92	0.06	A
		Night	12	1.02	0.12	A
	Summer	Day	152	0.53	0.04	A
		Night	58	0.24	0.61	B
	Winter	Day	7	0.75	0.17	A
		Night	3	0.70	0.25	A
fasciata	Spring/Fall	Day	67	1.12	0.10	A
		Night	6	1.31	0.19	A
	Summer	Day	48	1.20	0.11	A
		Night	21	1.20	0.12	A
	Winter	Day	7	0.88	0.18	A
		Night	4	0.31	0.22	B
rhombifera	Spring/Fall	Day	31	0.92	0.07	A
		Night	13	0.84	0.13	A
	Summer	Day	50	1.03	0.07	A
		Night	23	0.72	0.10	B
	Winter	Day	13	0.38	0.12	A
		Night	5	0.70	0.19	A

[a] LS means within each class with the same letter are not significant.

those observed in soil; TMO in water was not significantly different from air or soil (Table 7). There were no significant differences in TMO between microhabitats within each species. Interactions of microhabitat with light and season, however, show some interesting trends. Snakes observed in water were behaviorally thermoregulating 56.9% of the time (Table 7); this figure is not significantly different between day and night (Table 8). The LS means for snakes observed in air or soil, on the other hand, were significantly higher in the day than at night. In the day, thermoregulation was significantly higher in air than in water; at night, TMO was significantly higher in water than in soil.

In the summer, snakes observed in air or soil were in the thermally optimum microhabitat significantly more than those in water (Table 9). This holds true for both day and night (Table 10), although the difference is greater at night. In spring/fall, snakes in water showed the highest thermal microhabitat optimization, significantly more than in air or soil (Table 9). There is a pronounced diel difference in spring/fall (Table 10): day observations show no significant differences in TMO among microhabitats, all values being very high; at night thermoregulation in air and soil dropped to extremely low levels, while snakes in water showed almost complete thermoregulation. Snakes in air had a significantly higher TMO than those in soil in winter (Table 9). During the day in winter, thermoregulation in air was significantly greater than that in water or soil,

Table 7. TMO LS means for microhabitat as a main effect for three species of water snakes.

Microhabitat	N	LS mean	SE	Significance[a]
Air	166	0.65	0.08	A
Soil	80	0.41	0.11	B
Water	345	0.57	0.05	AB

[a] LS means with the same letter are not significantly different. (P>0.05).

Table 8. TMO values (LS mean ± SE (N)) for the light x microhabitat interaction for three species of water snakes.

Microhabitat	Light		Signif.[a]
	Day	Night	
Air	0.79 ± 0.07 (134)	0.52 ± 0.14 (32)	A B
Soil	0.64 ± 0.11 (63)	0.18 ± 0.17 (17)	A B
Water	0.58 ± 0.57 (249)	0.56 ± 0.07 (96)	A A
Signif.[a]	A AB B	AB A B	

[a] LS means within each class with the same letters are not significant (P>0.05).

Table 9. TMO LS means for season x microhabitat interactions for all snake species combined.

Season	Microhabitat	N	LS mean	SE	Signif[a]
Spring/Fall	Air	85	0.51	0.13	A
	Soil	6	0.31	0.23	A
	Water	109	0.91	0.60	B
Summer	Air	73	0.87	0.59	A
	Soil	67	0.83	0.08	A
	Water	212	0.40	0.05	B
Winter	Air	8	0.57	0.17	A
	Soil	7	0.09	0.60	B
	Water	24	0.40	0.10	AB

[a] LS means within each season with the same letter are not significantly different (P>0.05).

Table 10. TMO values (LS mean ± SE (N)) for season x light x microhabitat interactions for all snake species combined.

Season	Light	Microhabitat			
		Air	Soil	Water	Signif[a]
Spring/Fall	Day	0.80 ± 0.06 (82)	0.78 ± 0.19 (5)	0.84 ± 0.06 (82)	A A A
	Night	0.22 ± 0.24 (3)	0.17 ± 0.41 (1)	0.99 ± 0.09 (27)	A A B
Summer	Day	0.80 ± 0.06 (46)	0.91 ± 0.07 (54)	0.57 ± 0.05 (150)	A A B
	Night	0.93 ± 0.08 (27)	0.75 ± 0.12 (13)	0.22 ± 0.06 (62)	A A B
Winter	Day	0.75 ± 0.17 (6)	0.23 ± 0.21 (4)	0.32 ± 0.11 (17)	A B B
	Night	0.39 ± 0.29 (2)	0.05 ± 0.23 (3)	0.47 ± 0.15 (7)	A A A

[a] LS means within each row with same letter are not significantly different (P>0.05).

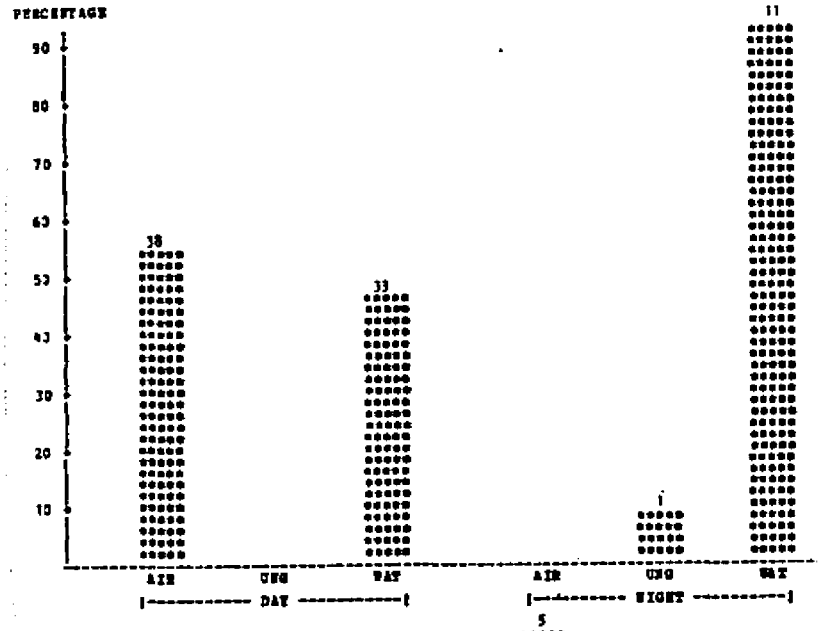
but there were no significant differences among microhabitats at night (Table 10).

Thermal Microhabitat Optimization Versus Microhabitat Use Patterns

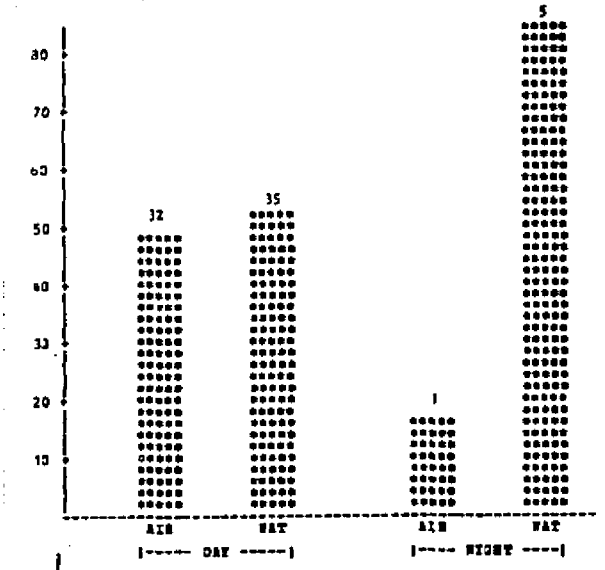
Diel variation in microhabitat use was consistent with behavioral thermoregulation. There was a significant avoidance of air and preference for water at night (X^2=16.7, P<0.05), when TMO values in air and soil were significantly lower (Table 8). In spring/fall there was a significant (X^2=16.7, P=0.0001) shift in microhabitat use between day and night (Fig. 1), which is consistent with the shift in behavioral thermoregulation (Table 10). Forty-four percent of the day observations were in water; at night, when air and soil had only negligible thermal microhabitat optimization, 88% of the observations were in water.

In the summer, when air and soil behavioral thermoregulation values were higher than water, 60% of the observations were in water (Table 9). This inconsistency is true for both day and night (Table 10). Snakes at night in the summer were in water for 62% of observations, even though the LS mean TMO in water was only 0.22, as opposed to 0.94 in air and 0.75 in soil. Snakes in the summer, then, were spending more time in water than would be predicted based on temperature.

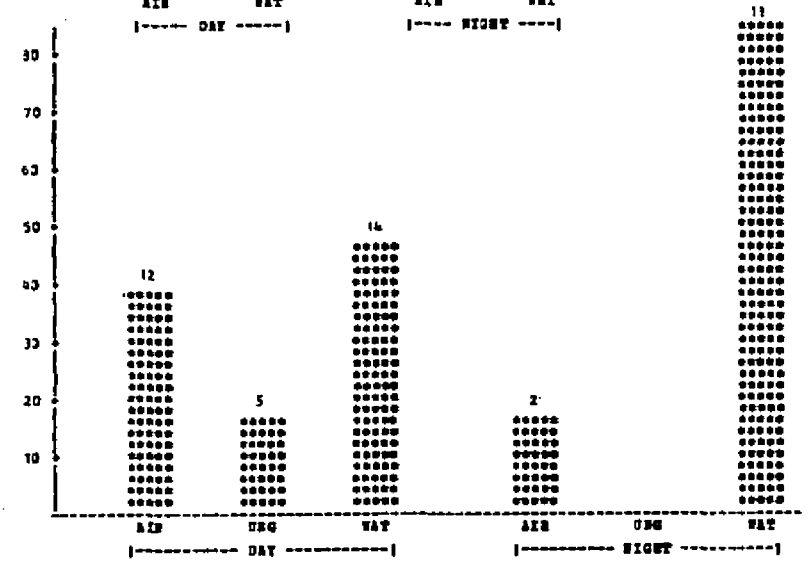
Fig. 1. Daily microhabitat use by three species of water snakes (Nerodia) in spring/fall; UNG = underground (soil), WAT = water.



cyclopion



fasciata



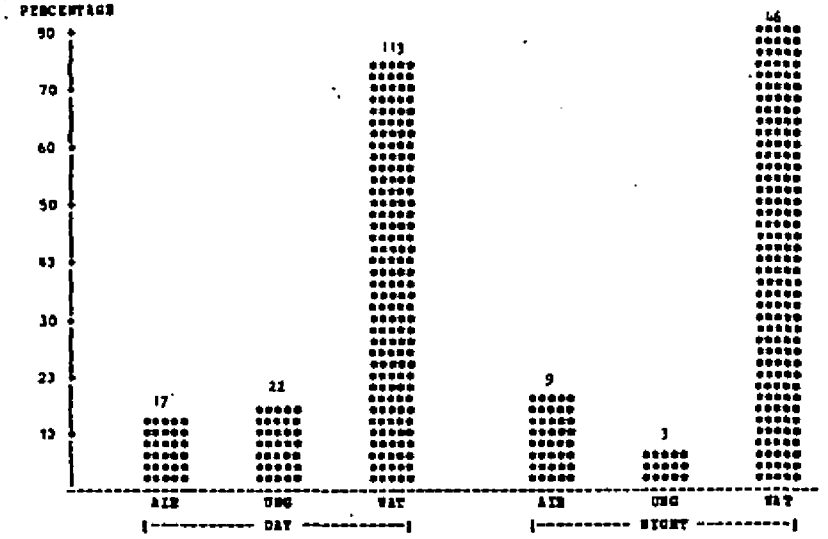
rhombifera

The question of microhabitat use in the summer becomes compounded when one considers that there was a significant difference in microhabitat frequencies between species (X^2=105.13, P=0.0001). A frequency histogram (Fig. 2) shows that each species had its own pattern of microhabitat use, and the patterns were identical for day and night. Nerodia cyclopion had a very high frequency in water. Nerodia fasciata showed a higher than expected occurrence in air, about equal to that in water, while N. rhombifera showed a significant preference for soil.

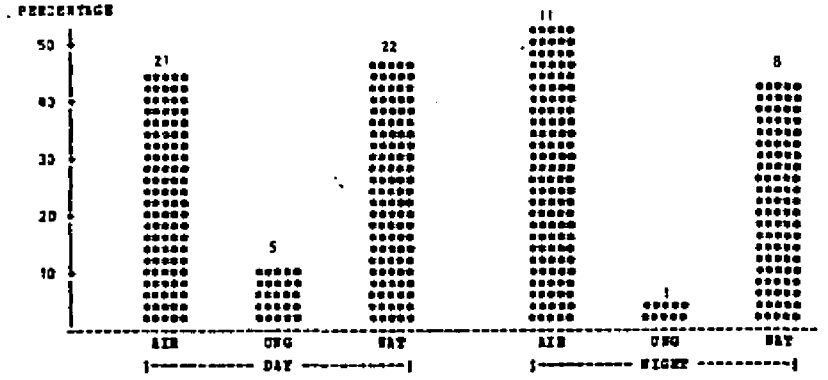
When the species x microhabitat interaction is considered for only summer observations, all three species show lowest behavioral thermoregulation in water (Table 11); the difference is not significant for Nerodia fasciata, which occurred in air and water in equal frequencies (Fig.2). The LS mean TMO for N. rhombifera in soil is significantly higher than in water (Table 11), and this species had a higher frequency in soil than in the other two microhabitats. The greatest inconsistency was in N. cyclopion, which was in the water for 72% of observations, but water was the optimum microhabitat in only 21% of those observations.

The inconsistency found in Nerodia cyclopion is even more striking when diurnal differences are considered. The trend holds true for both day and night, but the greatest inconsistency occurred at night: only 21% of the observations were in air or underground, when behavioral

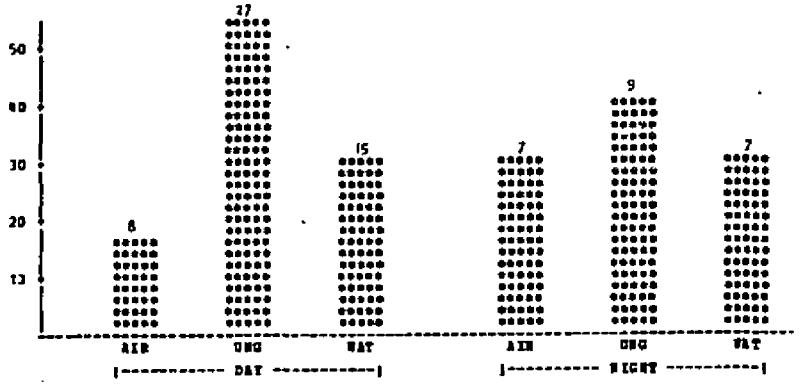
Fig. 2. Daily microhabitat use by three species of water snakes (Nerodia) in summer; UNG = underground (soil), WAT = water.



cyclopion



fasciata



rhombifera

Table 11. TMO LS means for species x microhabitat interactions, summer observations only for each of the three species of snakes.

Species	Microhabitat	N	LSmeans	SE	Signif[a]
cyclopion	Air	26	0.86	0.09	A
	Soil	25	0.86	0.13	A
	Water	159	0.21	0.05	B
fasciata	Air	32	1.06	0.10	A
	Soil	6	1.06	0.26	A
	Water	31	0.86	0.18	A
rhombifera	Air	15	0.88	0.11	AB
	Soil	36	0.90	0.10	A
	Water	22	0.67	0.10	B

[a] LS means within each species with the same letter are not significantly different (P>0.05).

thermoregulation was 91% (Table 12). The LS mean TMO in the water was only 0.03, but the frequency for this microhabitat was 79%. The animals in this group were spending a great deal of time in a microhabitat that was not thermally optimum.

BODY TEMPERATURE VARIATION

Relationship Between Body Temperature and Ambient Temperature

Only in Nerodia cyclopion was the the slope of body temperature (BT) versus ambient temperature (AT) significantly different from 1 (slope=0.80, r=0.88). This indicates some degree of control by the species that showed the lowest thermal microhabitat optimization. When seasonal differences are considered, N. cyclopion is again the only species that showed significant thermoregulation, with slopes of 0.60 (r=0.73) in spring/fall and 0.69 (r=0.64) in summer.

Results of the ANOVA on TX (Table 13) indicate unequal population means for the nine sources of variation (F=13.1, P=0.0001), and a significant amount of variation in the model was due to the main effects of weight class, sex, species, and temperature class, and to the interaction between species and temperature class.

Table 12. TMO LS means for microhabitat x light, Nerodia cyclopion in summer only.

Light	Microhabitat	N	LSmean	SE	Signif.[a]
Day	Air	17	0.76	0.10	A
	Soil	22	0.81	0.09	A
	Water	113	0.40	0.05	B
Night	Air	9	0.95	0.13	A
	Soil	3	0.91	0.22	A
	Water	46	0.03	0.07	B

[a] LS means within each light class with the same letter are not significantly different (P>0.05).

Table 13. Analysis of variance table for TX (=BT-AT) in *Nerodia cyclopion*, *N. fasciata*, and *N. rhombifera*.

Source	DF[a]	SS[b]	MS[c]	F[d]	P[e]
Model	15	832.1043	55.4736	13.01	0.0001
Error	574	2448.2510	4.2652		
Corrected Total	589	3280.3554			
Weight Class	1	84.7382		19.87	0.0001
Sex	1	36.0133		8.44	0.0038
Repr. Cond.	1	11.2534		2.64	0.1049
Sampling Method	1	1.8874		0.44	0.5062
Species	2	65.6241		7.69	0.0005
Temp. Class	2	46.0954		5.40	0.0047
Season	2	13.6532		1.60	0.2027
Light	1	5.6583		1.33	0.2499
Species x Temp. Cl.	4	77.4235		4.54	0.0013

[a] Degrees of Freedom

[b] Sums of Squares

[c] Mean Squares

[d] F-statistic

[e] Probability of erroneously rejecting the null hypothesis

Nerodia cyclopion showed thermal nonconformity by maintaining appropriate control in all three temperature classes (Table 14). This species was the only one to show control in the HIGH temperature class with an LS mean that was negative and significantly different from zero. Such thermal nonconformity is complementary to the low thermal microhabitat optimization shown for this species in summer. In the LOW temperature class, N. cyclopion kept its body temperature an average of 1.9 C above ambient, but in the MID range TX was not significantly different from zero. Nerodia fasciata showed significant control in the LOW range, but in the MID range, BT averaged 2.3 C warmer than AT, which was not thermally appropriate. N. rhombifera showed the most thermoconformity; the LS mean TX was not significantly different from zero in any temperature class.

Interaction Between Thermal Nonconformity and Thermal Microhabitat Optimization

Summer.

Summer was the only season in which differences in microhabitat use patterns between species were significant ($P=0.0001$), as is shown in Figure 2. These patterns did not differ between day and night ($P>0.05$). It was pointed out earlier that Nerodia cyclopion spent a disproportionate amount of time in the water, which resulted in low thermal

Table 14. TX Least Squares (LS) means for three species of water snakes by temperature class (TEMPCL).

Species	TEMPCL	N	LS Mean	SE	P[a]
cyclopion	HIGH	179	-0.58	0.29	0.0477
	LOW	23	1.90	0.46	0.0001
	MID	100	0.27	0.27	0.3034
fasciata	HIGH	9	0.46	0.85	0.5868
	LOW	30	1.30	0.60	0.0311
	MID	114	2.28	0.54	0.0001
rhombifera	HIGH	13	-0.91	0.65	0.1621
	LOW	42	-0.11	0.33	0.7442
	MID	80	-0.57	0.34	0.0956

[a] Probability of erroneously rejecting the null hypothesis that LS mean = 0.

microhabitat optimization (38.5%) during this season. When thermal nonconformity is considered (Table 15), it is apparent that the snakes were keeping their body temperatures significantly lower than ambient when in water. Thermal nonconformity also occurred during the day in the HIGH temperature class when snakes were in soil. Microhabitat optimization was indicated in all other categories, with the exception of day/air/high, where TX was in the appropriate direction, but not significant. The difference is significant ($P<0.05$) when day/air/high observations from spring are combined with those from summer ($N=13$).

In the day, then, when Nerodia cyclopion is in air or soil, it may be using either type of thermoregulation, whereas in the water thermal nonconformity is used almost exclusively. At night, microhabitat optimization is used when out of the water, and nonconformity when in water, which is 79% of the time. This species seems to be able to spend most of its time in the water, even though it is not thermally optimal, by some sort of thermal nonconformity.

In the summer Nerodia fasciata occurred in air and water in almost equal amounts of time (Fig. 2), and was rarely found in soil. In fact, this species was found in air significantly more frequently than were the other two species. This pattern is reflected in the high degree of thermal microhabitat optimization, and complete absence of thermal nonconformity. Nerodia fasciata spent almost all

Table 15. Mean TX (=BT-AT) and TMO for various categories of light x microhabitat x temperature class for Nerodia cyclopion during the summer.

Light	Micro-habitat	Temp. Class	N	TX Mean	TX SE	TMO Mean	TMO SE	Type[a]
Day	Air	High	7	-1.02	0.63	0.57	0.14	
		Mid	10	0.21	0.53	0.90	0.12	1
	Soil	High	10	-1.83	0.53	0.70	0.12	2
		Mid	12	-0.32	0.48	1.00	0.14	1
	Water	High	105	-1.25	0.16	0.33	0.04	2
		Mid	8	-1.25	0.59	1.00	0.13	1
Night	Air	High	1	-0.63	1.67	1.00	0.38	1
		Mid	8	3.82	0.59	1.00	0.13	1
	Soil	High	3	-0.84	0.97	1.00	0.22	1
	Water	High	45	-0.78	0.25	0.00	0.06	2
		Mid	1	-1.27	1.67	1.00	0.38	1

[a] Type of thermoregulation: 1 = thermal microhabitat optimization, 2 = thermal nonconformity.

of its time in a microhabitat that was within its thermal preferendum.

Nerodia rhombifera, when compared with the other species, showed a significant preference for soil and avoidance of water (Fig. 2). Although snakes in a number of categories showed no thermoregulation at all, microhabitat optimization was indicated in those with large samples, and the overall TMO was high (88%; Table 5). Thermal conformity was shown in summer by this species. Behavioral thermoregulation in the day was significantly higher than at night (Table 6) probably due to the lack of thermoregulation in the water at night.

Spring/Fall

As pointed out earlier, microhabitat use patterns in spring/fall were consistent with behavioral thermoregulation, which was highest for all species during this season (Table 5). There was a significant diel difference in microhabitat use with a preference for water and avoidance of air and soil at night. This pattern was consistent ($P>0.05$) for all species; their microhabitat frequency distributions (Fig. 1) are almost identical.

During the day Nerodia cyclopion was in water only when it was thermally optimal. More than half of the day observations were in air (Fig. 1) where both types of thermoregulation were used. When air temperature was in the

preferred range (58% of the day/air observations), thermal microhabitat optimization was shown and TX was not significantly different from zero. When AT was high, BT was kept an average of 3.6 C cooler; when AT was below the preferred range, BT was kept 3.3 C warmer. At night, thermal microhabitat optimization was achieved by staying in water. This species again seemed to use both types of thermoregulation in a complementary fashion.

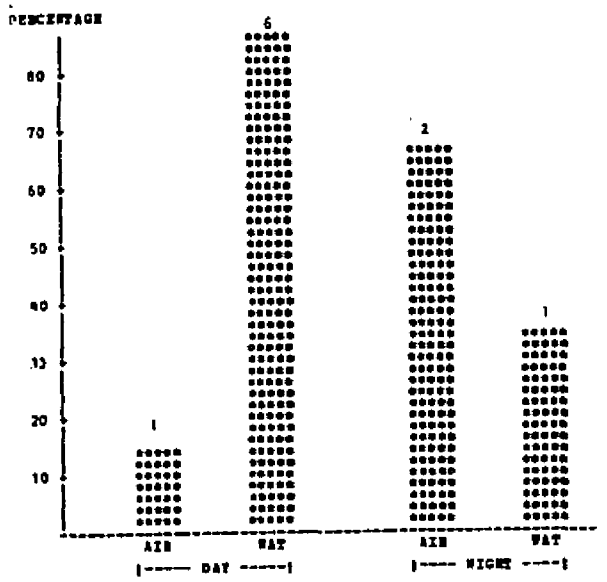
Nerodia fasciata again showed no thermal nonconformity. During the day, a high degree of thermal microhabitat optimization occurred in the air; in the water, however, no significant thermoregulation occurred in the HIGH or LOW ranges, which comprised almost half the observations. Night microhabitat optimization was very high; most observations were in water (Fig. 1).

Both types of thermoregulation were indicated in the day/air/low category for N. rhombifera. A high degree of thermal microhabitat optimization was shown for both day and night.

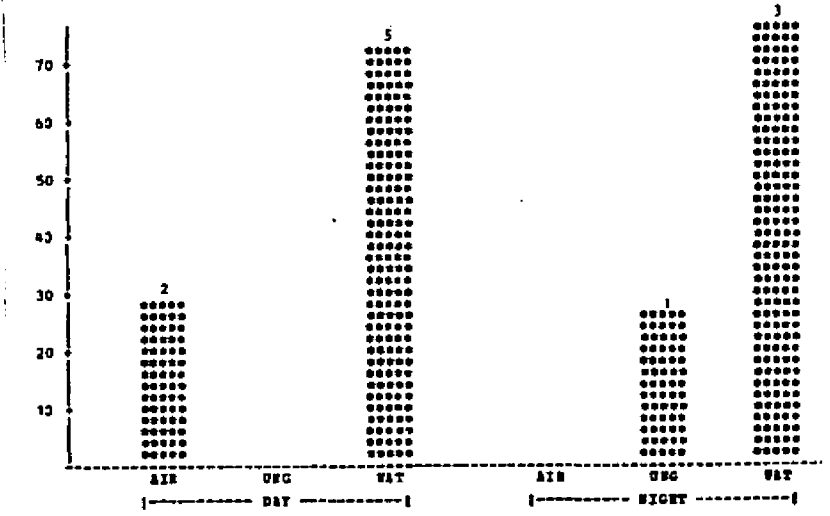
Winter

When day and night observations are combined, there is no significant difference in winter microhabitat use between species; all species were most frequently observed in water (Fig. 3). There was, however, a difference in thermoregulation. Nerodia cyclopion showed signficant thermal

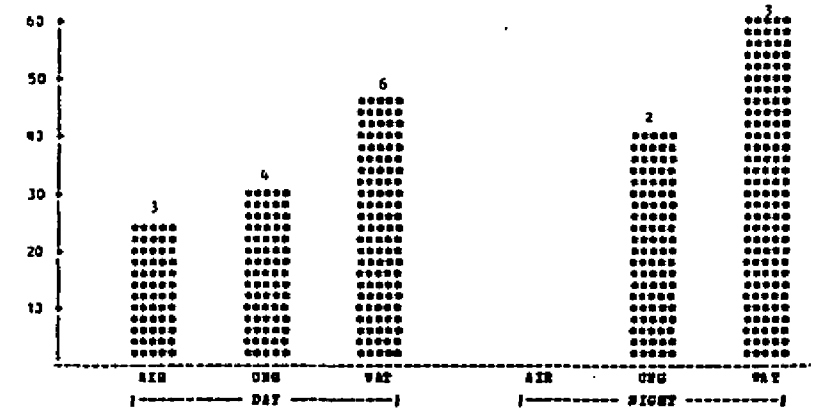
Fig. 3. Daily microhabitat use by three species of water snakes (Nerodia) in winter; UNG = underground (soil), WAT = water.



cyclopion



fasciata



rhombifera

microhabitat optimization in both air and water, whereas TMO was indicated only in air for N. fasciata and N. rhombifera. Nerodia fasciata indicated thermal nonconformity in water; none of the other positive TX means was significant. Thermal microhabitat optimization in winter was significantly higher than in summer for N. cyclopion, but both other species had their lowest microhabitat optimization in winter.

Although the significance of diel differences in microhabitat could not be assessed due to small sample sizes, Nerodia cyclopion seemed to show a shift, whereas the other two species did not (Fig. 3). In the day, N. cyclopion showed both types of thermoregulation in air; microhabitat optimization is generally shown in the water.

Nerodia fasciata was found most frequently in water during both day and night (Fig. 3). Although thermal microhabitat optimization was not shown in water, thermal nonconformity occurred at night. In the day, air observations indicated both types of thermoregulation; no thermoregulation occurred in water. Overall thermal microhabitat optimization for N. fasciata in winter was 59%, and this was the only season where thermal nonconformity was indicated.

Nerodia rhombifera was found in air only in the day (Fig. 3), but use of soil and water was similar during day and night. Air use in the day indicated both types

of thermoregulation, but soil and water use did not seem to be temperature dependent. No thermoregulation was shown in soil in the day or night, and water was optimum only at night. Overall winter thermal microhabitat optimization for N. rhombifera was 54% in winter.

Summary of species differences

There was a significant (P=0.0001) difference in the frequency distribution of each species among temperature classes (Table 16), which reflected different thermoregulatory responses. Nerodia cyclopion had a much higher frequency than expected in the HIGH class but lower than expected in both MID and LOW. Thermal nonconformity, in lieu of thermal microhabitat optimization, was used in the summer to allow use of the water microhabitat, which was not thermally optimal. In other seasons this species exhibited a high degree of both types of thermoregulation. Nerodia fasciata used a high degree of thermal microhabitat optimization to try to remain in its thermal preferendum, as evidenced by the higher than expected occurrence in the MID range, and lower than expected in the HIGH. Nerodia rhombifera also avoided the HIGH temperature class, and was in the MID range slightly more than expected. The higher than expected occurrence in the LOW class may be related to the use of solar radiation, but overall thermoregulation in this category was low.

Table 16. Contingency table showing relationships between water snake species and temperature classes (X^2=186.8, P=0.0001).

Species	Frequency	Temperature Class			Total
		HIGH	LOW	MID	
cyclopion	Observed	180*	24*	100*	304
	Expected	104	49	151	(51%)
	Row Percent	59	8	33	
fasciata	Observed	9*	30	114*	153
	Expected	52	25	76	(26%)
	Row Percent	6	20	74	
rhombifera	Observed	13*	42*	80	135
	Expected	46	22	67	(23%)
	Row Percent	10	31	59	
Total	Observed	202	96	294	592
	Row Percent	34	16	50	100%

* The observed frequency is significantly different from the expected frequency.

Solar Effects

During the day in the LOW temperature class, snakes in air showed significant thermal nonconformity regardless of sun visibility. Snakes observed during the night in air in the LOW temperature class showed thermal conformity. The correlation between TX and percent sun (on the animal's body) was significant ($P<0.01$) only in the LOW temperature class (Fig. 4), where a positive relationship was shown.

Even though the direct effect of solar radiation may be to elevate BT, the snakes were apparently able to maintain some control over this effect. Solar radiation may have been employed in the LOW temperature class when the sun was visible, but a high TX was also maintained when the sun was not visible. In the MID and HIGH temperature classes, the effect of solar radiation on BT was repressed.

Time Effects

Figure 5 shows the fluctuations in body, air, and water temperatures for an individual over a 24 h period. One can see by this graph that the snake kept BT fairly constant and more or less within its preferred range.

When the relationship between AT and BT for consecutive observations (i and i+1) within a 24 h period are considered in the form of a flow diagram (Fig. 6), the number of combinations or "pathways" by which snakes reached a

Fig. 4. Regression of TX (=BT-AT) versus percent sun on the snake's body (PCTSUN) by temperature class.

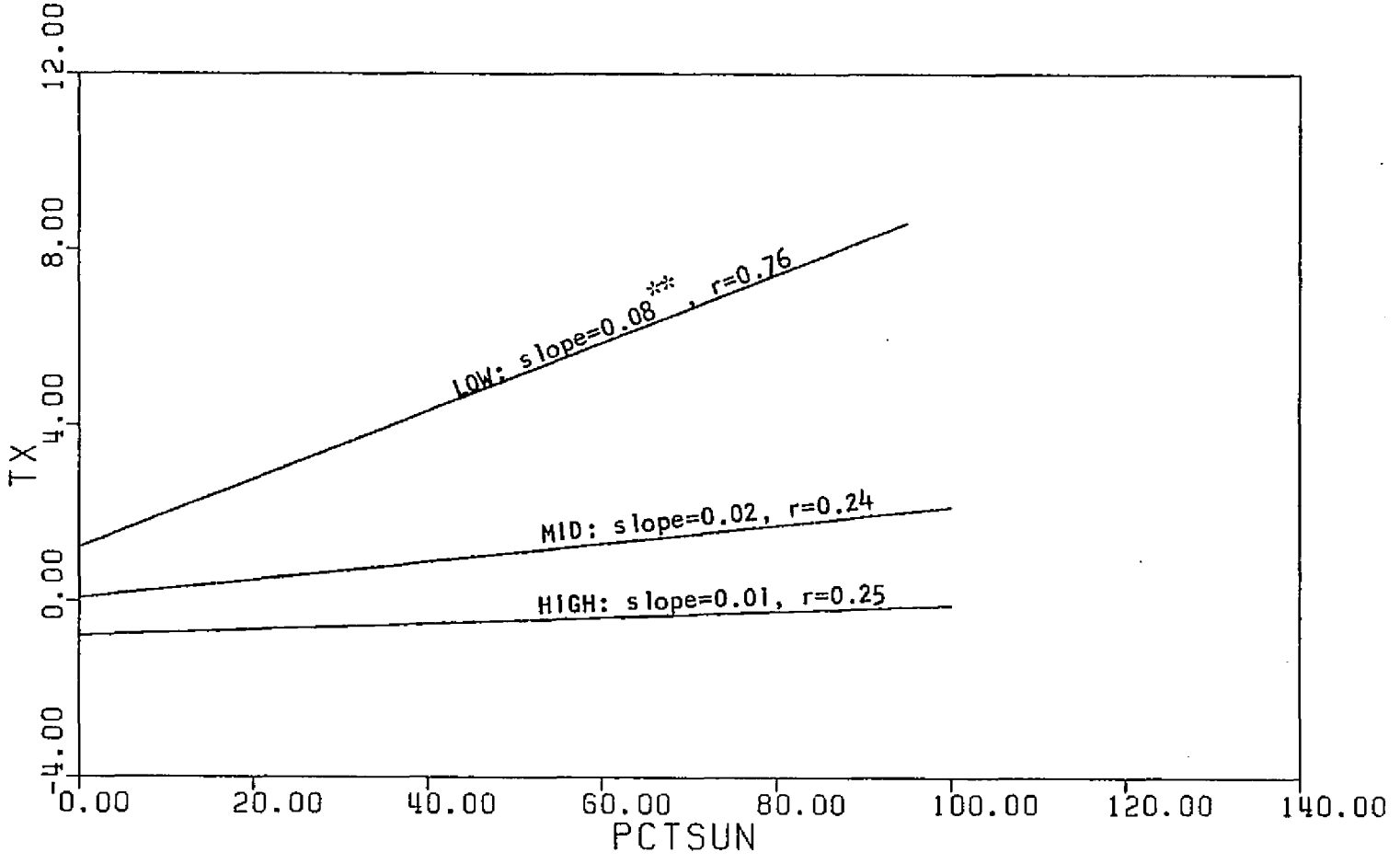

12.00
8.00
4.00
0.00
-4.00
TX
LOW: slope=0.08** , r=0.76
MID: slope=0.02, r=0.24
HIGH: slope=0.01, r=0.25
0.00
20.00
40.00
60.00
80.00
100.00
120.00
140.00
PCTSUN

Fig. 5. Temperature fluctuations over a 24 h period for Nerodia cyclopion #2300. YDTIME = "year-day.time" (218.5 = 9 August at noon).

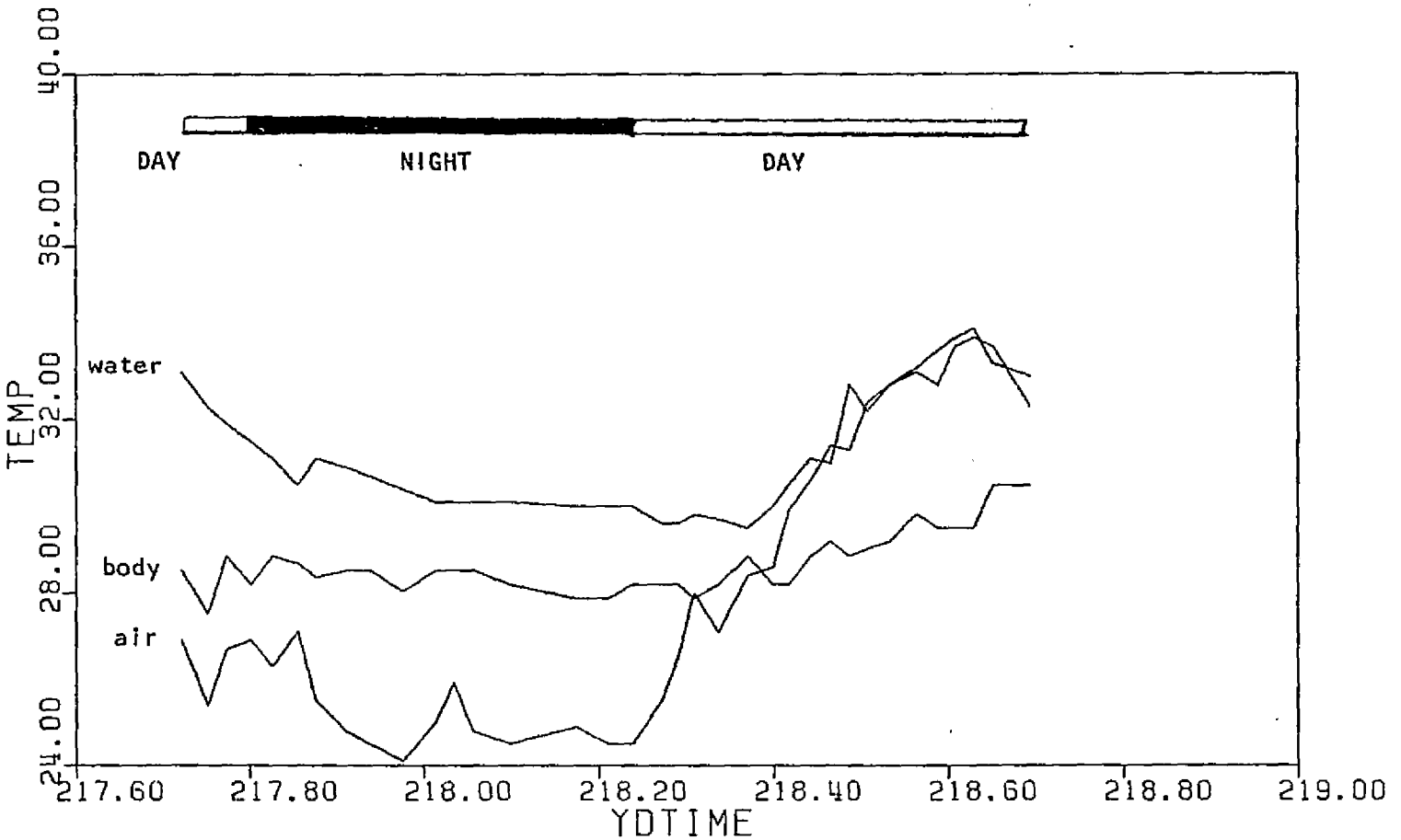
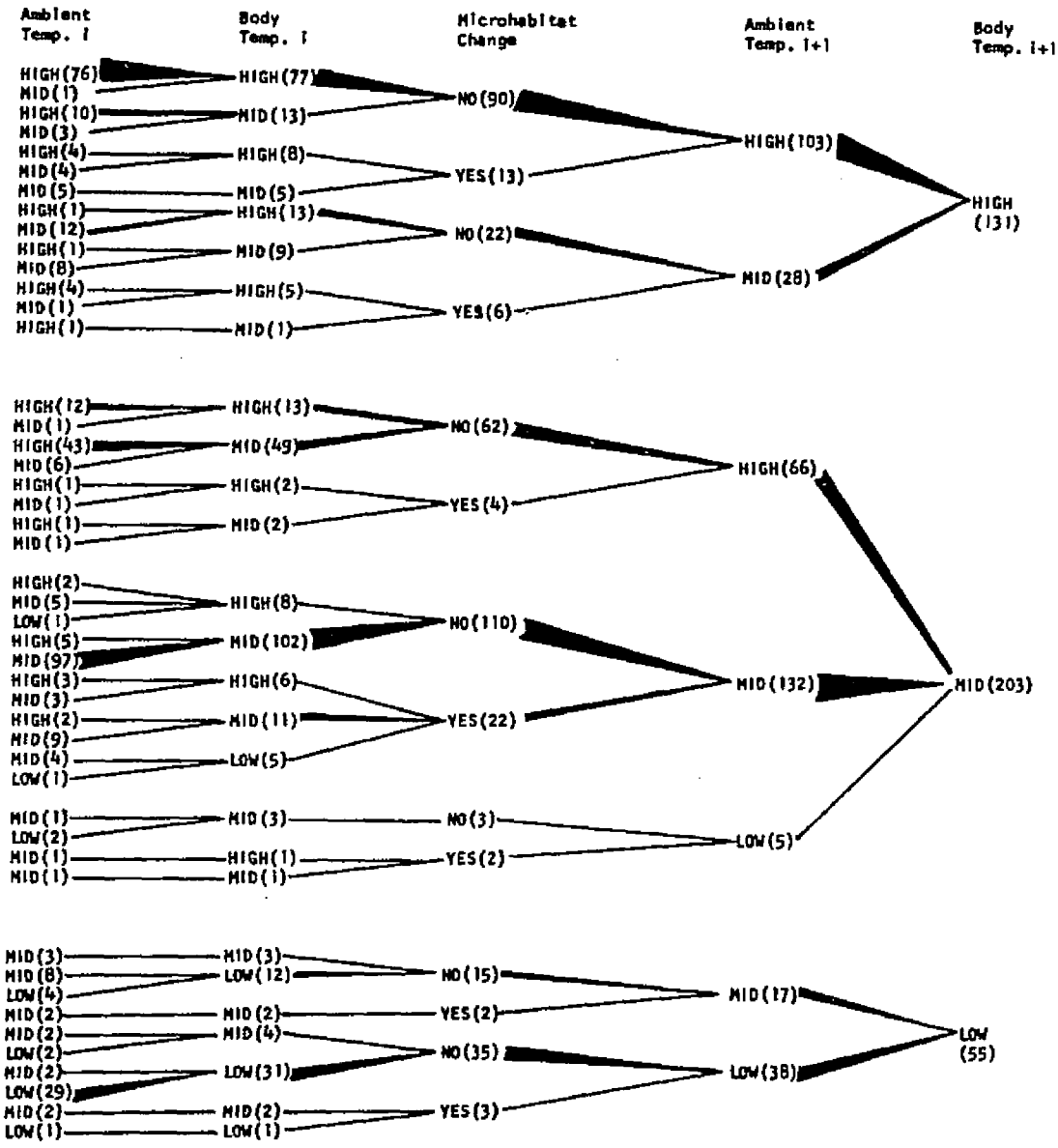

DAY
NIGHT
DAY
water
body
air
TEMP
40.00
36.00
32.00
28.00
24.00
217.60
217.80
218.00
218.20
218.40
218.60
218.80
219.00
YDTIME

Fig. 6. Relationship of snake body temperature and ambient temperature for two consecutive observations (i and i+1) within a 24 h period.


Ambient Temp. t
Body Temp. t
Microhabitat Change
Ambient Temp. t+1
Body Temp. t+1
HIGH(76)
MID(1)
HIGH(10)
MID(3)
HIGH(4)
MID(4)
MID(5)
HIGH(1)
MID(12)
HIGH(1)
MID(8)
HIGH(4)
MID(1)
HIGH(1)
HIGH(77)
MID(13)
HIGH(8)
MID(5)
HIGH(13)
MID(9)
HIGH(5)
MID(1)
NO(90)
YES(13)
NO(22)
YES(6)
HIGH(103)
MID(28)
HIGH (131)
HIGH(12)
MID(1)
HIGH(43)
MID(6)
HIGH(1)
MID(1)
HIGH(1)
MID(1)
HIGH(13)
MID(49)
HIGH(2)
MID(2)
NO(62)
YES(4)
HIGH(66)
HIGH(2)
MID(5)
LOW(1)
HIGH(5)
MID(97)
HIGH(3)
MID(3)
HIGH(2)
MID(9)
MID(4)
LOW(1)
HIGH(8)
MID(102)
HIGH(6)
MID(11)
LOW(5)
NO(110)
YES(22)
MID(132)
MID(203)
MID(1)
LOW(2)
MID(1)
MID(1)
MID(3)
HIGH(1)
MID(1)
NO(3)
YES(2)
LOW(5)
MID(3)
MID(8)
LOW(4)
MID(2)
MID(2)
LOW(2)
MID(2)
LOW(29)
MID(2)
LOW(1)
MID(3)
LOW(12)
MID(2)
MID(4)
LOW(31)
MID(2)
LOW(1)
NO(15)
YES(2)
NO(35)
YES(3)
MID(17)
LOW(38)
LOW (55)

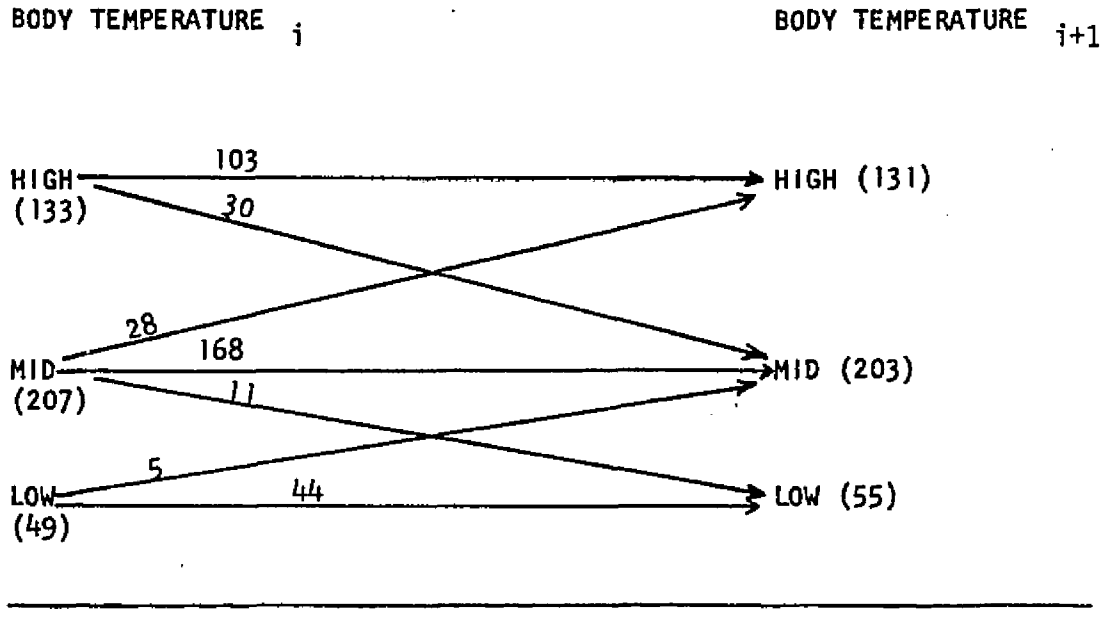
given BT_{i+1} class is striking. It is also noteworthy that in many instances BT and AT were in different temperature classes, and this relationship often changed from one observation to the next. Despite the apparent complexity of such a diagram, the majority of observations in each group seems to show inertia, i.e., no change from one observation to the next.

Body temperature variation over time

The results of considering only BT (Fig. 7) show that the number of observations in each class for i is almost identical to that for i+1. However, it is not always the same snakes which remain in a given class; there is a relatively high frequency of changing from one class to another. This pattern is reflected in the mean change in BT and AT for snakes in the HIGH temperature class. Snakes that started out with AT_i and BT_i in HIGH showed a significant decrease in AT and BT between i and i+1. Those who ended up with both AT_{i+1} and BT_{i+1} in HIGH, however, showed a significant increase in AT and BT between i and i+1, i.e., they came from a cooler temperature (both body and ambient). This suggests that the snakes may be staying in the HIGH class for only short periods of time.

When the distribution of species in the three classes of BT_{i+1} are considered, significant differences are

Fig. 7. Changes between snake BT_i and BT_{i+1}. Numbers indicate sample size.


BODY TEMPERATURE i
BODY TEMPERATURE i+1
HIGH (133)
MID (207)
LOW (49)
HIGH (131)
MID (203)
LOW (55)
103
30
28
168
11
5
44

detectable (X^2=36.9, P=0.0001). Nerodia cyclopion had a higher than expected frequency in the HIGH temperature class, and lower than expected in LOW. Nerodia fasciata occurred as expected in all classes. Nerodia rhombifera avoided the HIGH class, but showed a preference for LOW.

Thermoregulatory categories

The frequency distributions within the three thermoregulatory categories are significantly different (X^2=36.3, P=0.0001) between species (Table 17). Nerodia cyclopion had a higher than expected frequency in the thermal nonconformer category and lower than expected in the thermoconformer group. Both N. fasciata and N. rhombifera showed a preference for thermoconformity and an avoidance of nonconformity. The frequencies in the nonregulator category were not significantly different between species.

Effect of microhabitat change

Of the 28 instances of microhabitat change in thermoregulators (24 additional instances were in nonregulators), only eight (15%) showed thermokinesis. All were Nerodia cyclopion; five were thermoconformers, and three thermal nonconformers. It is possible, however, that a microhabitat change may be thermally beneficial in a more subtle way (e.g., different modes of heat exchange in air versus water) and not show gross differences based on temperature classes.

Table 17. Contingency table for three species of water snakes and three thermoregulatory categories (X^2=36.3, P=0.0001).

Category	Frequency	Species			Total
		cyclopion	fasciata	rhombifera	
Conformer	Observed	49*	36*	28*	113
	Expected	72	23	18	(29%)
	Row Percent	43	32	25	
Non-	Observed	125	31	30	186
regulator	Expected	119	38	30	(48%)
	Row Percent	67	17	16	
Non-	Observed	74*	12*	4*	90
conformer	Expected	57	18	14	(23%)
	Row Percent	82	13	4	
Total	Observed	248	79	62	389
	Row Percent	64	20	16	100%

* The observed frequency is significantly different from the expected frequency.

When BT_i is in the HIGH or LOW temperature class, snakes that change microhabitats have a significantly (X^2=20.2, P=0.0001) better chance of reaching a MID BT_{i+1} than those that stay in the same microhabitat (Fig. 8). When BT_i is in MID, however, those that do not change microhabitats have a higher frequency in MID BT_{i+1} (X^2=9.2, P=0.002) than those that do. Thus optimization theory would predict that, based on probability, snakes would be more apt to change microhabitats when BT_i is in LOW or HIGH than MID. Even so, the percentage of microhabitat change between classes of BT_i is not significantly different (X^2=1.8, P=0.40). When the ambient temperature class is considered, however, differences appear. When AT_i is in the MID range, those observations with BT_i in HIGH or LOW show significantly higher microhabitat change than those whose BT_i is in MID (X^2=6.7, P=0.019). There is no significant difference in microhabitat change for HIGH and LOW AT_i classes (X^2=1.8, P=0.18). Thus a snake is most likely to change microhabitats when the ambient temperature is in the preferred (MID) range, and body temperature is outside of the preferred range.

Eccritic Body Temperatures

Only Nerodia fasciata showed an eccritic temperature (27.2 C) that was not significantly different from its preferred temperature (Table 18). Nerodia cyclopion had

Fig. 8. Effect of microhabitat change on relationship between BT_i and BT_{i+1}. Numbers indicate sample size.

Body Temperature i	Microhabitat Change	Body Temperature i+1

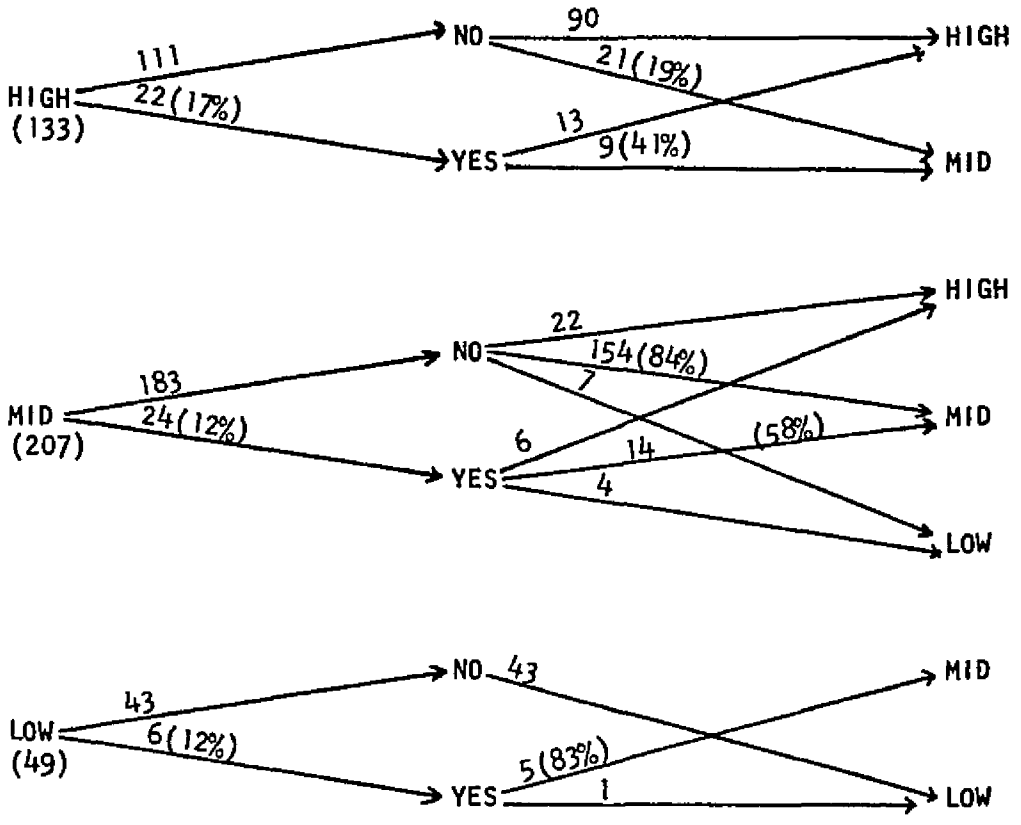


Table 18. Eccritic and preferred temperatures (in degrees Celsius) for three species of Nerodia.

Species	Eccritic			Preferred[a]		
	N[b]	MBT[c]	SE	N	MBT	SE
cyclopion	304	27.36	0.23	250	25.16	0.20
fasciata	153	27.18	0.40	253	27.12	0.23
rhombifera	135	25.18	0.44	230	27.29	0.24

[a] from Walley and Mushinsky (in press)

[b] N = number of observations

[c] MBT = mean body temperature

a mean body temperature (27.4 C) that was 2 C warmer than its lab MBT, while the eccritic temperature for N. rhombifera (25.2 C) was 2 C cooler than its preferred temperature. The eccritic temperatures for N. cyclopion and N. fasciata were not significantly different, but both were significantly ($P<0.05$) higher than that of N. rhombifera.

All three species showed a summer MBT which was significantly higher than winter (Table 19). In summer, both Nerodia cyclopion and N. fasciata had significantly higher MBTs than N. rhombifera, but in spring/fall and winter there were no significant interspecific differences. Nerodia cyclopion and N. fasciata showed no significant diurnal differences; N. rhombifera had a lower MBT at night than in the day in spring/fall and winter, but no difference for summer.

Table 19. Mean body temperatures (MBT) for each species of Nerodia by season.

Species	Season	N	MBT	SE
cyclopion	Spring/Fall	72	23.54	0.35
	Summer	222	29.07	0.16
	Winter	10	16.88	1.71
fasciata	Spring/Fall	16	23.83	1.03
	Summer	126	28.59	0.30
	Winter	11	15.81	1.74
rhombifera	Spring/Fall	44	24.33	0.51
	Summer	73	27.70	0.41
	Winter	18	17.01	1.20

SPATIAL ECOLOGY

LAND/WATER RELATIONS

Comparison of mean distance from land/water interface and water depth values for the species x season interaction is shown in Table 20. In the winter, Nerodia rhombifera had a mean distance from the land/water interface that was not significantly different from zero while the other two species were found in open water. When N. rhombifera was in water in winter, its depth was significantly greater than that for N. fasciata ($P<0.05$). In spring/fall N. rhombifera was in open water ($P<0.01$) and N. cyclopion and N. fasciata were found at the land/water interface. The mean depths in spring/fall were not significantly different between species; in day only, however, N. cyclopion was in deeper water than N. rhombifera. In summer all three species were found at the land/water interface. When in water, N. rhombifera was at a greater depth than N. cyclopion or N. fasciata ($P=0.0001$).

Within water levels a general pattern is apparent. During low water, Nerodia cyclopion and N. fasciata were found at the land/water interface ($P>0.05$), while N. rhombifera was on dry land ($P<0.05$). When in water, however, the latter species was found at a greater ($P<0.05$)

Table 20. LS means for distance (in meters) from land/water interface and depth (in centimeters) of water for three snake species for each season.

Species	Season	Distance			Depth		
		N	LS Mean	SE	N	LS Mean	SE
cyclopion	Spring/Fall	75	10.84	8.15	60	40.31	4.92
	Summer	172	- 4.94	4.90	142	12.48	3.02
	Winter	10	51.70	16.76	10	30.86	10.75
fasciata	Spring/Fall	69	0.53	13.75	51	37.94	10.62
	Summer	64	10.73	12.03	39	2.98	9.66
	Winter	11	92.52	16.39	10	12.22	12.54
rhombifera	Spring/Fall	39	26.57	8.33	24	35.30	6.33
	Summer	70	8.61	8.08	20	51.17	7.53
	Winter	18	-18.68	10.66	8	45.29	9.40

depth than N. fasciata during low water. When water level was high, all three species were found in open water, and N. rhombifera was in deeper water than the other two ($P<0.05$). There were no interspecific differences in depth during the day, but the preference of N. rhombifera for deep water was again significant at night ($P<0.01$).

Nerodia cyclopion was found in deeper water in spring/fall than in summer (Table 20), and N. fasciata in spring/fall was in deeper water than in summer or winter. There were no seasonal differences in depth for N. rhombifera.

During high water, snakes were generally observed in open water, whereas they were more frequently found at the land/water interface during low water. Snakes in the water, however, were found at the same mean depth in high or low overall water levels ($P>0.05$). This indicates that, when water level is low, snakes may move toward inundated areas; otherwise they would have been found on dry land during low water. When water is high, however, they do not seem to seek the land/water interface, but remain in open water.

Within species, Nerodia cyclopion and N. fasciata were found at the land/water interface during low water and in open water during high. Nerodia rhombifera was also in open water during high water, but was found on dry land ($P<0.05$) during low water, which indicates a possible lack of compensatory movements in this species. Nerodia cyclopion was

in significantly deeper water during low water levels ($P<0.05$), whereas the other species showed no differences in depth.

There were no diel differences in distance from the land/water interface. In addition, there was no significant difference in depth. Diel differences are apparent, however, within species. Nerodia cyclopion and N. fasciata were found in open water during the day ($P<0.001$) and at the land/water interface at night ($P>0.05$). Nerodia rhombifera was generally found at the land/water interface during the day ($P=0.07$), and in open water at night ($P<0.05$).

There were no diel differences in distance from the land/water interface during summer or winter; in spring/fall, the animals were found in open water during the day and at the land/water interface at night. Nerodia cyclopion in winter was in open water during the day and at the land/water interface at night. Nerodia fasciata in spring/fall was in open water during the day and at the land/water interface at night. Nerodia rhombifera in winter was on dry land during the day ($P<0.01$) and at the land/water interface at night ($P>0.05$). In spring/fall N. rhombifera was in open water at night and at the land/water interface during the day.

During high water, snakes were found in open water during both day and night. When water level was low, snakes

were in open water during the day ($P<0.05$), and at the land/water interface at night ($P>0.05$). Diel differences in depth were practically nonexistent.

LINEAR MOVEMENT PATTERNS

Movement Rates

The distance moved per day ranged from zero to 424 m, but the distribution was highly skewed to the right (skewness=+3.27); 50% of the observations had values of less than 10 m/day. The overall mean movement rate was 9.55 m/day ($=10^{0.98}$ m/day). Least squares means for levels of sex, reproductive condition, and weight class showed no significant differences.

Least squares means for species show that Nerodia fasciata had a significantly higher rate of movement than did N. rhombifera ($P<0.05$); the LS mean for N. cyclopion was not significantly different from either of the other two. Interspecific differences within seasons were significant only in spring/fall, when N. fasciata moved significantly more than did the other two species; movement rates in summer and winter were not different between species. There were no significant interspecific differences during high water. During low water N. fasciata again showed a significantly greater rate of movement than either of the other species ($P<0.05$).

There was no significant difference in movement rates between high and low water levels. This statement also holds true when water level differences are considered within species and within season.

No significant differences were found among seasonal movement rates when all observations are considered. Within species, however, Nerodia fasciata showed significant differences in movement rate among seasons; this species moved more in spring/fall than in summer or winter. The other two species showed no significant difference in seasonal movement rates. It is worth noting that all snakes continued to move throughout the winter, although movements were decreased. No individual was known to remain at one location (hibernaculum) for the entire winter; all moved frequently. During high water, the movement rate in winter was significantly lower than in spring/fall ($P<0.01$) or summer ($P<0.05$), but seasonal differences were not significant during low water.

Results of the regression analysis indicate that the slopes of the eight regression lines are unequal ($F=4.16$, $P=0.0002$). The low r^2 value (0.18) reflects the high degree of variation in the dependent variable. The only sources of variation with slopes that were significantly different from zero were photoperiod ($P=0.05$) and distance from the land/water interface ($P=0.003$); both slopes were positive (Table 21). There was a trend toward increased movements as day length increased, but no corresponding relationship with temperature was seen. Snakes on dry land showed the least movement, and a general increase in movement rate was found as distance

Table 21. Slopes for each of the eight independent variables from the analysis of variance on the dependent variable "log of distance moved per day."

Variable	Slope
Photoperiod	0.142 *
Max./Min. Temp. Mean	-0.004
Max./Min. Temp. Range	-0.008
Water Level	-0.019
Water Level Change	0.052
Distance From Land/Water Interface	0.004 *
Dis. From Land/Water Interface Change	0.002
Max./Min. Temp. Mean x Range	-0.002

* Slope significantly ($P<0.05$) different from zero.

from the land/water interface increased. Movement rates were not correlated with the change in distance from land/water interface, water level, or the change in water level.

Daily Activity

Activity occurred in 17.3% of the 341 observations that were less than 12 h apart. There was no significant difference (X^2=1.37, P=0.50) in the relative number of active individuals among day, night, and twilight (within one hour of sunrise or sunset) samples. This is also true within species and season. The animals seemed to show no set activity pattern, but moved randomly relative to time of day.

PLANAR MOVEMENT PATTERNS

Home Range

Areas and other pertinent information for individual snakes are presented in Table 22. I found a great deal of variation in home range size, with values ranging from 0.003 ha (30 m^2) to 15.4 ha. Elliptical estimates were generally less than polygonal areas, and showed less variation between individuals. The mean areas (Table 23) were 5.7 $\pm$ 1.3 (SE) ha (polygon) and 3.2 $\pm$ 0.6 ha (ellipse); the two means were not significantly different from each other. The mean home range length (maximum distance between two points) was 554 $\pm$ 107 m.

The small number of individuals and high degree of variation make it difficult to rule out the role of chance in any observed differences between groups. Student's t-tests showed no significant differences in mean home range sizes (both methods) within the variables species, sex, and reproductive condition; none of the trends shown (Table 23) were consistent enough to rule out chance ($P>0.05$). In addition, neither body weight, the median month during the tracking period, the mean interval between observations, nor the total number of days that each individual was monitored was found to be significantly correlated with home range size (both methods).

Table 22. Home range areas and pertinent information on individual snakes monitored for more than 15 days.

Tag	Species	Sex[a]	Wt.[b]	Months[c]	Days[d]	Int.[e]	N	Home Range[f]		
								Poly.	Ellip.	Length
2000	cyclopion	GF	607	7- 7	18.9	0.44	43	3.499	3.425	434
3475	fasciata	GF	291	8-10	47.9	3.68	13	4.644	3.062	433
4285	fasciata	NF	260	4- 7	70.9	1.16	61	7.812	3.101	650
4287	fasciata	GF	337	4- 7	86.7	1.28	68	14.713	7.089	620
4299	cyclopion	GF	472	6- 7	47.0	1.57	30	15.394	7.284	1684
4364	cyclopion	GF	797	6- 7	30.9	2.06	15	5.552	4.632	462
4399	rhombifera	M	318	6- 7	36.1	1.06	34	1.089	0.602	175
5298	rhombifera	M	390	7- 2	228.0	4.39	52	6.624	2.972	659
5567	rhombifera	GF	858	8-11	100.6	3.35	30	2.779	0.867	682
5568	cyclopion	NF	223	9-10	36.3	4.04	9	0.003	0.003	16
6273	fasciata	NF	207	11- 2	107.1	6.95	11	1.495	2.845	460
6277	cyclopion	NF	536	11- 3	142.6	1.02	11	7.255	3.846	475
6283	cyclopion	GF	289	3- 7	112.5	2.74	41	3.156	1.360	454

(footnotes on next page)

Table 22 (continued).

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[a] GF= gravid female, NF= nongravid female, M= male

[b] Weight in grams

[c] Months of the year during which the snake was monitored

[d] Number of days the snake was monitored

[e] Mean interval (days) between observations

[f] Polygon and ellipse are areas in hectares; length is in meters

Table 23. Mean home range sizes for snakes by sex, reproductive condition, and species. Polygon and ellipse are areas in hectares.

Class	Level	N	Polygon		Ellipse	
			Mean	SE	Mean	SE
All Observations		13	5.69	1.34	3.16	0.62
Sex	Female	11	6.03	1.51	3.41	0.69
	Male	2	3.86	2.77	1.79	1.19
Repr.	Gravid	7	7.11	2.08	3.76	2.54
Cond.	Nongrav.	6	4.05	1.45	2.23	1.54
Species	*cyclopion*	6	5.81	2.16	3.42	1.04
	fasciata	4	7.17	2.83	4.02	1.02
	rhombifera	3	3.50	1.64	1.48	0.75

These results were obtained by an analysis of variance and show no consistent trend. For instance, although snakes with the largest home ranges (tag nos. 4287 and 4299) were tracked between April and July, other snakes tracked during this period had home ranges that were considerably smaller, and some animals monitored during other times of year had large home ranges. Habitat conditions throughout the study area were fairly homogeneous in relation to the above home range sizes. In fact, there was considerable spatial overlap between individual ranges. Hence no individual was confined to a certain habitat type such that the home range sizes would reflect differences in habitat.

Movements Within Home Range

Usually a major movement resulted in the establishment of a new home area; this occurred in 25 (47%) of the 53 major movements in my study. Eight major movements (15.1%) were to a previously established home area, and five (9.4%) were transitory (followed by another major movement). An additional 15 (28.3%) major movements resulted in the census being terminated due to capture or death of the snake, or loss of the radio signal.

The mean interval between major movements was 17.4 days (Table 24), and the mean distance moved was 301.3 m.

Table 24. Means and other statistics pertinent to major movements and home areas of snakes.

Variable	N	Mean	SE	Min.[a]	Max.[b]	Skewness
Areas[c]	16	2.3	0.3	1.0	5.0	+0.98
Btw/moves[d]	52	17.4	3.8	0.7	166.9	+3.71
Distance[e]	36	301.3	41.3	123.0	1290.0	+2.54
Days[f]	44	20.2	4.3	0.7	166.9	+3.49

[a] Minimum value

[b] Maximum value

[c] Number of home areas per individual

[d] Interval between major movements (in days)

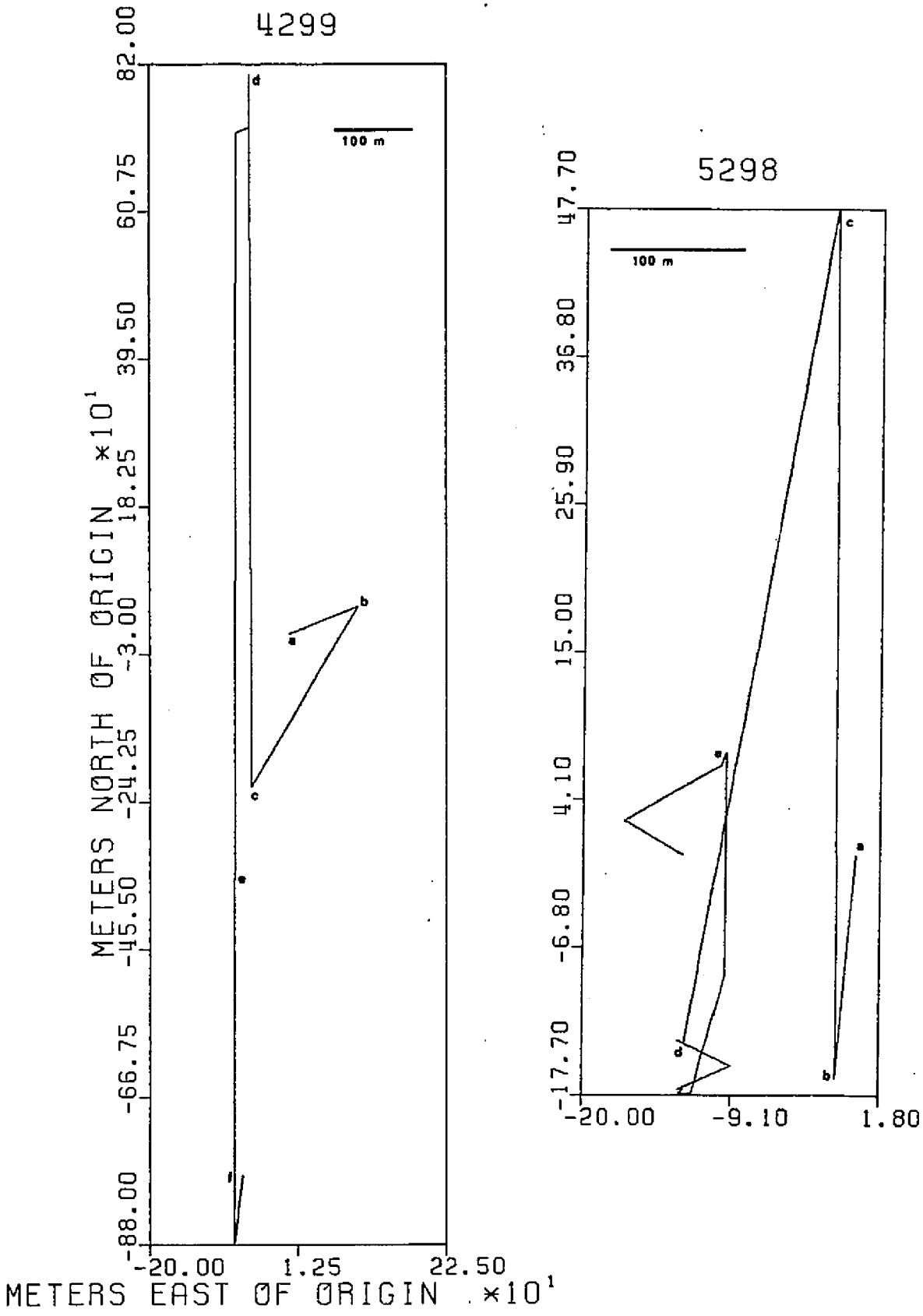
[e] Distance of major movements (in meters)

[f] Number of days spent in a home area

Again a high degree of variation in movement data is apparent, and the distributions are positively skewed. The number of home areas per individual ranged from one to five (mean=2.3), and snakes remained in a home area for an average of 20.2 days.

The individual that stayed in a home area for the greatest length of time was a male Nerodia rhombifera, tag no. 5298 (Fig. 9). He was released at point "a" on 11 July 1978 and was found at point "b" 1.3 days later, a major movement of 165 m. The snake remained at point "b," within a six square meter area under the overhang of the bank of Bayou Braud, for 17 days, then moved 635 m northward along the bayou to point "c." After four days at point "c" the snake moved 625 m southward again to point "d," a crayfish hole on a high ridge of ground. He was found in that same spot from 9 August to 21 October. In fact, he was thought to be dead underground, since the animal was not seen until 18 October, when I found him basking on the ground near the hole on a cool, clear autumn afternoon. The snake was relatively inactive and in moulting condition. When he was released after capture, he circled around a tree then came back toward me and entered a hole less than one meter from where I was sitting. This indicates a high degree of familiarity with the home area, since he had to risk moving toward a potential predator in order to find the entrance to a known refugium.

Fig. 9. Movement maps of individual snakes, nos. 5298 and 4299. Numbers at top indicate tag numbers, letters refer to major movements and home areas (see text).


4299
5298
100 m
100 m
82.00
60.75
39.50
18.25
-3.00
-24.25
-45.50
-66.75
-88.00
47.70
36.80
25.90
15.00
4.10
-6.80
-17.70
-20.00
1.25
22.50
-9.10
1.80
METERS NORTH OF ORIGIN *10¹
METERS EAST OF ORIGIN *10¹

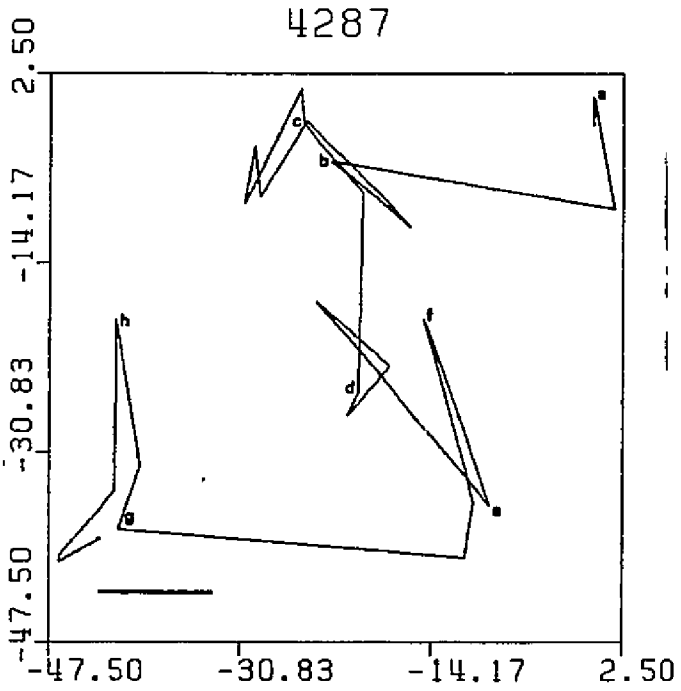
That individual (#5298) remained in the vicinity of point "d" for nearly 167 days. He stayed mostly underground, but was seen lying on the surface of the ground on a number of occasions. The snake lost 135 g between 11 July and 28 December. He made a major movement and was found at point "e" on 27 January 1979. He stayed in that home area until I lost the signal in late February. This animal had three home areas ("db", "ea" and "c") and four major movements within a home range polygon of 6.6 ha.

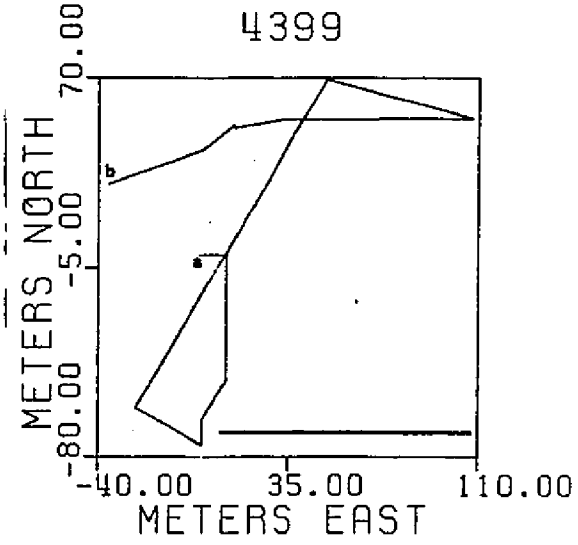
The snake with the largest home range (15.4 ha polygon) was a gravid female Nerodia cyclopion, #4299 (Fig. 9). Her home range was practically linear in shape, corresponding to a long, straight section of Bayou Braud. This animal had the greatest range length (1.7 km), the longest single major movement (1.3 km), the shortest mean interval between major movements (7.3 days), and was one of two individuals with the maximum number of home areas (5). She was released at point "a" (Fig. 9) on 8 June 1978 and was found at point "b" the next day. That was the only time she was found more than 25 m from the shore of Bayou Braud. She stayed in home area "ab" for 3 days, then moved to point "c," a major movement of 300 m. After 5 days in area "c," a major movement of 950 m was made to point "d." Ten days later the snake moved 1290 m to point "e," stayed there for two days, then made another major movement to home area "f," where she remained until the census was terminated 17 days later.

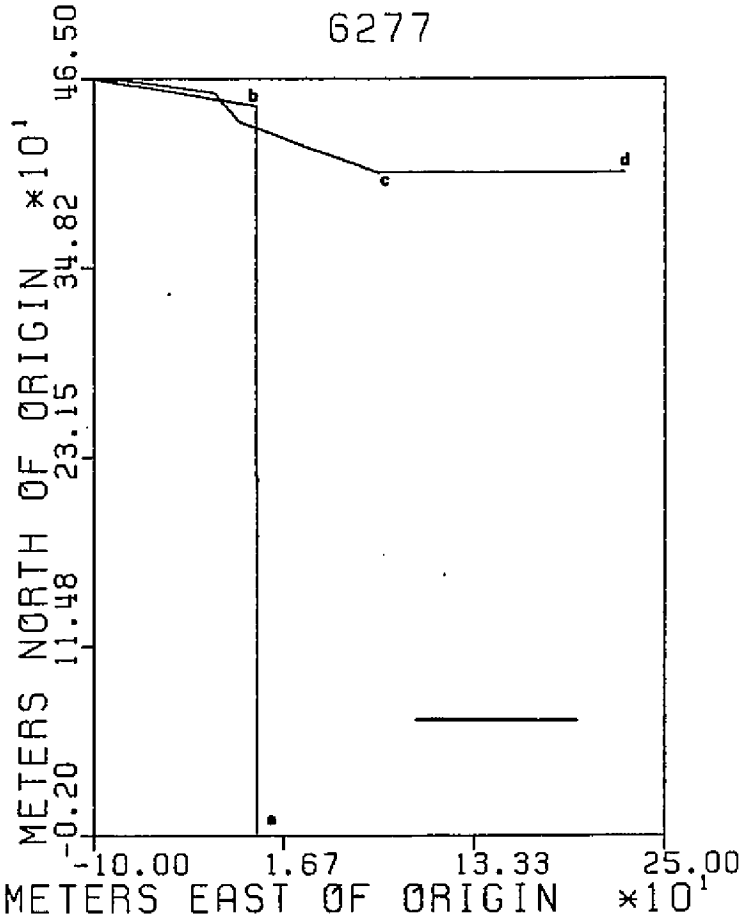
A female Nerodia fasciata, #4287 (Fig. 10), also had five home areas, and showed the greatest number of major movements (9). I released her on 26 April 1978 at point "a," where she stayed for eight days before moving to area "b." A number of minor movements were made within home area "b," where she remained for 13 days. During this time I observed her copulating on 16 May at point "c." The two snakes were in an entanglement of vines (Brunnichia scandens) one meter above the surface of the water, and were observed in copulation for more than one hour. This reinforces the contention that the presence of a transmitter does not seem to cause any significant behavioral alterations in these animals. The snake stayed in area "d" for 18 days, area "e" for 3 days, then moved to point "f" (considered in same home area as "d"), then back to "e" a day later. After nine days in area "e," she moved to area "g," moved to point "h" (a transitory point) 7 days later, then moved back to "g," remaining for 21 days before I lost the signal. I noted that she was gravid on 14 June (at point "e"), but never had the opportunity to capture her after that.

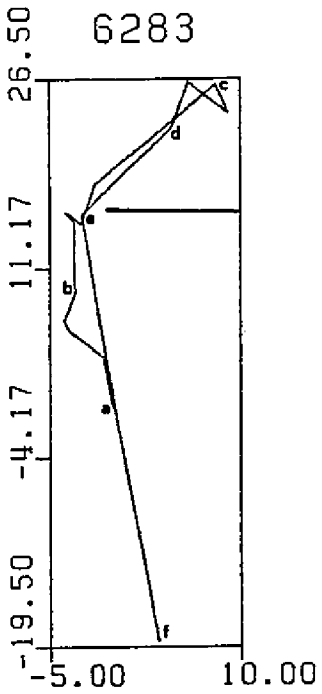
The snake with the smallest home range, Nerodia cyclopion #5568, stayed within a 30 m^2 home area for 36 days, after which time I was unable to pick up a signal. Although the home range size probably would have increased

Fig. 10. Movement maps of individual snakes, nos. 4287, 4399, 6277, and 6283. Numbers at top indicate tag numbers, letters refer to major movements and home areas (see text); scale line=100 m.


4287
2.50
-14.17
-30.83
-47.50
-47.50
-30.83
-14.17
2.50


4399
70.00
-5.00
-80.00
METERS NORTH
-40.00
35.00
110.00
METERS EAST


6277
46.50
34.82
23.15
11.48
-0.20
METERS NORTH OF ORIGIN *10¹
-10.00
1.67
13.33
25.00
METERS EAST OF ORIGIN *10¹


6283
26.50
11.17
-4.17
-19.50
-5.00
10.00

had I been able to continue monitoring over a longer period, another N. cyclopion (#4364) exhibited a home range of 5.6 ha over a 31-day period. In addition, the snake with the largest home range (#4299) was monitored for only 47 days.

Another animal whose home range contained only one home area was a male Nerodia rhombifera, #4399 (Fig. 10). He was released at point "a" on 20 June 1978 and showed considerable movement, but never was observed more than 100 m from a previous point. He was most frequently found underground or perched in a tree, sometimes at heights of 2-3 m. He was observed for the last time at point "b" 36 days after release.

A female Nerodia cyclopion, #6283, was released at point "a" (Fig. 10) on 31 March 1979 and monitored continuously for a 24 h period, at the end of which she was observed at point "b." The snake remained in home area "ab" for 24 days before making a major movement to point "c." She was observed in area "c" for 14 days, after which an intensive search of the surrounding area over many weeks failed to produce a signal. The area was monitored periodically after that, but I had already given up on locating her. Then, during a routine check on 18 July, more than two months after the last observation, I located the snake at point "d," 40 m from the last observation. Apparently she

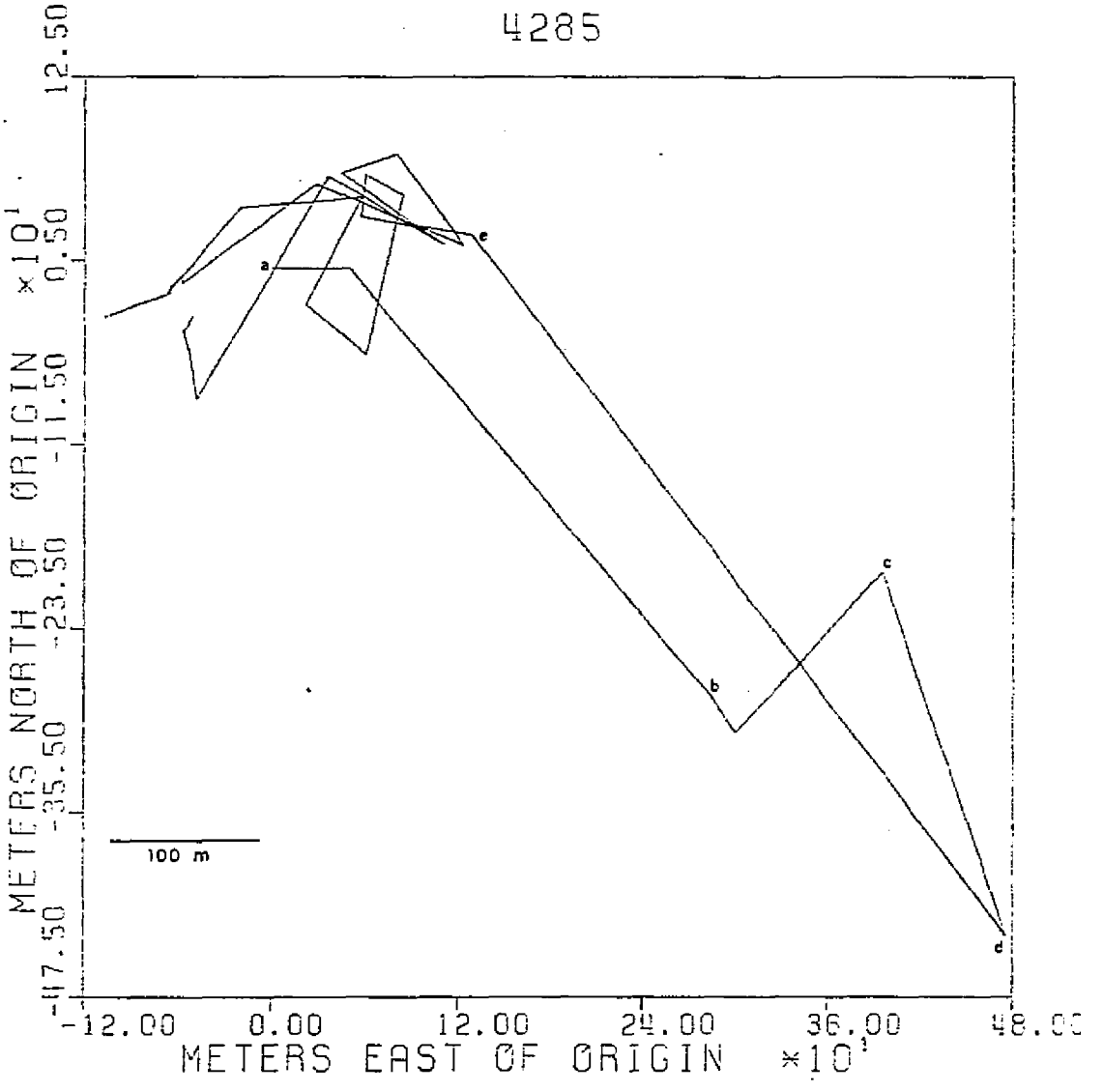
had moved out of the area and had, by chance, evaded my search before returning to the home area. Temporary transmitter failure is possible but unlikely. She was found at the same spot (point "d") 32 h later, then moved to point "e" within 11 h. I captured her at point "f" 14 h after that. The last two movements totaled 450 m in a 25 h period, the highest rate of movement I recorded.

Another snake whose signal was temporarily lost for more than thirty days was a female Nerodia cyclopion, #6277 (Fig. 10). She was released at point "a" on 9 November 1978, and moved to point "b" 5 days later. She stayed in that home area for 71 days, but I lost her after 17 January 1979 (point "c"). Her signal was received again on 31 March, 2.5 months later, and traced to a crayfish hole at point "d." I monitored the signal at that exact spot until 21 September 1979, at which time the ground was dry enough to excavate (it had been under 100 cm of water at one time). I found the transmitter 50 cm below the surface of the ground, still transmitting, but a thorough washing and search of the surrounding mud at the laboratory failed to reveal any snake body parts.

The greatest number of minor movements within a home area was shown by a female Nerodia fasciata, #4285 (Fig. 11). She was released at point "a" on 26 April 1978. She made a major movement to point "b" the next day, stayed there for four days, then moved to transitory points "c" and

"d" before returning to the original home area at point "e." Many movements were made back and forth between apparently familiar locations within this home area, where the snake remained for 59 days before the signal was lost.

Fig. 11. Movement map for individual no. 4285. Letters refer to major movements and home areas (see text).


4285
12.50
0.50
-11.50
-23.50
-35.50
-47.50
METERS NORTH OF ORIGIN ×10¹
100 m
a
b
c
d
e
-12.00
0.00
12.00
24.00
36.00
48.00
METERS EAST OF ORIGIN ×10¹

DISCUSSION

There are two basic mechanisms by which an ectotherm can regulate its body temperature. One is by being in a microhabitat the temperature of which is in or near its preferred range. I have referred to this phenomenon as thermal microhabitat optimization, and it does not require any adjustment in the BT/AT relationship. Thus TMO is largely a behavioral phenomenon and can occur in a complete thermoconformer. The second type of thermoregulation involves altering the relationship between body and ambient temperatures (thermal nonconformity) when AT is outside of the preferred range. Thermal nonconformity implies the use of physiological as well as behavioral processes, but not necessarily (see below). I must point out that observed phenonmena that are interpreted as thermoregulatory may often be explained by alternative hypotheses (see Heath 1964). Huey and Pianka (1977) acknowledged alternative hypotheses, but added that regardless of the cause of such behaviors, they inevitably have thermoregulatory effects.

Nerodia fasciata used thermal microhabitat optimization almost exclusively. This species was typically found in the optimal microhabitat and rarely exhibited any degree of thermal nonconformity. It usually made significantly greater use of optimal microhabitats than did either of the other species. As a result, N. fasciata kept its body temperature in the preferred range a high percentage of the time.

Nerodia rhombifera and N. cyclopion both showed considerable seasonal variation in thermal microhabitat utilization. Nerodia rhombifera was found in the optimal microhabitat 88% of the time in spring/fall and in summer, but significantly less often in winter. This species also showed some degree of thermal nonconformity when ambient temperatures were low, but only in the air during the day (it probably was using solar radiation). Nerodia cyclopion showed considerable thermal microhabitat optimization in spring/fall and in winter, but was found in an optimal microhabitat in only 39% of the summer observations. On the other hand, this species consistently showed thermal nonconformity in both high and low ambient temperatures. When AT was high, thermal nonconformity was shown in all three microhabitats (air, underground, and water), whereas in low AT it occurred in air only. Mushinsky et al. (1980) looked at the slope of BT x AT in five species of water snakes and found that N. cyclopion was the only one showing thermal nonconformity. They also stated that perching N. cyclopion captured in spring/fall sometimes had a BT four to seven degrees above air temperature.

The mechanism or mechanisms by which these snakes maintained a significant TX (=BT-AT) is not readily apparent from my data. Both Nerodia rhombifera and N. cyclopion showed a positive TX in air in the day when AT was below the preferred temperature range. It seems likely that solar radiation was the basis for thermal nonconformity in this case.

Only in LOW temperature class was TX positively correlated with the percentage of the body exposed to sunlight; snakes exposed to full sun in HIGH temperature class had no significant TX. It could be that snakes in cool temperatures were orienting their bodies more perpendicularly to the sun's rays, or a seasonal difference in the angle of the sun may be involved (Huey and Pianka 1977). Bakken (1976) reported that an inanimate object in thermal equilibrium with its environment may attain a TX of 5-10 C simply from changes in microtopography and orientation of the object.

That Nerodia cyclopion maintained a negative TX when AT was high, became a thermoconformer when AT was in its preferred range, and showed a positive TX when AT was low, indicates a high degree of thermoregulation. All three of these adjustments occurred in the air during spring/fall. Even more interesting is the fact that thermal nonconformity in the HIGH temperature class occurred in both air and water, which have different modes of heat transfer. Conduction and, to some extent, convection are the primary means of heat exchange in water; these, plus radiation and evaporation, are important in air (Crawshaw 1979). Since small reptiles have no significant metabolic heat production (Terpin et al. 1979), thermal nonconformity is achieved mainly by controlling the rate of heat exchange between the body core and environment (Kubb et al. 1980).

When an ectotherm changes from one ambient temperature to another, the core BT eventually reaches equilibrium with

AT (Reynolds 1979). The time required to reach equilibrium, or thermal time constant (Kubb et al. 1980), is determined by the rate of heat exchange between BT and AT. The rate of heat exchange is a function of environmental factors, physical characteristics of the animal's body, and active or passive physiological adjustments (Porter et al. 1973). A further complication is the fact that different parts of the body often have different thermal time constants (Kubb et al. 1980, Beitinger et al. 1977, Reynolds 1977, Erskine and Spotila 1977). The longer the thermal time constant, the longer an animal can stay in an AT that is not optimal by maintaining a significant TX.

Many animals exhibit thermal hysteresis, a significant difference in heating versus cooling rates (Crawshaw 1979). One reason for such a difference lies in cardiovascular adjustments: in many animals the cutaneous blood vessels dilate when heated and contract when cooled (Morgareidge and White 1969, Grigg and Alchin 1976, Smith et al. 1978). These cardiovascular adjustments affect thermal conductivity at the body surface, which results in a fast heating rate and slow cooling rate; thus most vertebrate ectotherms heat faster than they cool (Crawshaw 1979, Fry 1967). The marine iguana (Amblyrhynchus cristatus), for instance, heats twice as fast as it cools, thus it can rapidly accumulate heat by basking on rocks, then forage for an extended period in the cold water while the BT slowly drops (Bartholemew 1966). Other animals that accumulate heat more rapidly than it is

lost are alligators (Smith 1976, Terpin et al. 1979), lizards (Bowker and Johnson 1980, Bartholemew and Tucker 1963, Heath 1965, Bartholemew et al. 1965), some fish (Crawshaw 1976), and some turtles (Spray and May 1972, Voight and Johnson 1977). The mud puppy (Necturus maculosus, Anderson and Beitinger 1979) and bass (Micropterus salmoides, Kubb et al. 1980) showed heating and cooling at the same rate.

In order for thermal hysteresis to result in a negative TX during high ambient temperatures, as for Nerodia cyclopion in this study, the cooling rate would have to be faster than the heating rate. Thus the snake could cool down quickly, then move to a warm AT and stay there for a long time while the core BT slowly increased. My data do show that these snakes may be moving in and out of high ambient temperatures. Also, N. cyclopion was the only species in which microhabitat changes could definitely be interpreted as thermokinetic.

Spray and May (1972) reported that the cooling rate exceeded heating rate in two species of terrestrial turtles. The ratio of cooling rate to heating rate (c/h) was 2.2 in Terrepene carolina and 1.4 in Gopherus polyphemus. High c/h ratios allowed these turtles to remain active in hot weather. Spray and May used data of Moler (1970) and reported that the water snake Nerodia taxispilota had a c/h ratio of 1.06-1.37 in air and 1.07-1.17 in water. In addition, Spray and May (1972) calculated that the cooling rates of N. taxispilota and the two terrestrial turtles were about equal to that of terrestrial lizards, but the heating rates were distinctly lower than

in the lizards. They concluded that the terrestrial turtles exhibited active control of cooling rates, but not heating rates, since the heating rate in dead turtles was not different from that in the living animals. It is entirely possible, then, that N. cyclopion may be able to actively control its cooling rate and maintain a negative core BT in high ambient temperatures.

Another factor that may have an influence on thermal nonconformity in Nerodia cyclopion is the difference in BT in different parts of the body. Crawshaw (1979) stated that these different temperatures are determined by a complex weighting of thermal environments encountered in the recent past. Head-body temperature differences may be of particular significance because of the importance of the brain in thermoregulation, and some squamates are known to regulate head temperature more closely or precisely than that of the body core (Hammerson 1977, Heath 1964, Webb and Heatwole 1971, Dill 1972, Crawford 1972, Webb et al. 1972, Johnson 1972, 1973, Webb and Witten 1973, DeWitt 1967, Crawshaw 1976). Others claim that head-body temperature differences result from physical factors (Pough and MacFarland 1976, Georges 1979) or that peripheral temperatures are of equal importance (Spray and May 1972, Hammel et al. 1967). Snakes in water often keep their heads above the surface, presumably to facilitate breathing, but perhaps thermoregulatory functions are served as well. When the air is cooler than the water, as was often the case for N. cyclopion in the summer,

it may be possible to keep the emergent head cooler than the body. The role of evaporative cooling, either through the skin or by means of respiration, cannot be ruled out although processes such as panting in lizards (DeWitt 1967) or gaping in crocodilians (Smith 1979) have not been reported for snakes. Panting occurs in lizards when the BT exceeds 43 C (DeWitt 1967), well above the 39-40 C critical thermal maximum for Nerodia (Walley and Mushinsky in press). I found no difference in TX between snakes with the head above the surface and those completely submerged although the former were seen mostly in summer (87%) and the latter in cooler months (only 31% in summer). The observed seasonal difference fits both an oxygen- and a temperature-regulation hypothesis.

Despite the high degree of thermal nonconformity in Nerodia cyclopion, the mean core BT in the field (eccritic temperature) was still 2 C warmer than the laboratory preferred temperature (Walley and Mushinsky in press). Mushinsky et al. (1980) found a mean cloacal BT of 27.2 in the field, essentially the same as in this study. Nerodia rhombifera also showed a difference between eccritic and preferred temperatures, but the field MBT (25.2 C) was 2 C cooler than the lab value. Other field studies reported values that coincide with the preferred temperature: 27.5 (Mushinsky et al. 1980), 27.5 (Preston 1970), and 26.9 C (Brattstrom 1965). The low MBT in my study may be related to the frequent use of the underground habitat (35% of my N.

rhombifera observations) by this species. These snakes would not have been censused by field studies using methods other than radiotelemetry. Nevertheless, the animals maintained in the lab gradient had an opportunity to keep their BT at 25 C but still chose 27 C, which indicates a real difference between eccritic and preferred temperatures. The summer MBT for N. rhombifera in this study was 27.7 C, close to the MBT of the active snakes reported in other studies.

Nerodia fasciata, the species with the highest degree of thermal microhabitat optimization, had equal lab and field temperatures (27.1 C and 27.2 C, respectively). Mushinsky et al. (1980) found a slightly cooler field MBT (26.2 C, N=197). The above relationships in eccritic and preferred temperatures are also reflected in the relative frequencies in HIGH, MID and LOW temperature classes, both for AT and BT. Nerodia fasciata was found more often than expected in the MID class, N. cyclopion more than expected in HIGH, and N. rhombifera more than expected in LOW.

If the final preferendum concept (Fry 1947) is valid, then a difference between lab and field temperatures would imply an overall decreased performance in body functions. Even though most functions undoubtedly were acclimatized to the field temperatures, the acclimatized rate would presumably be less than optimal with considerable variation in the degree of acclimatization in different processes (Prosser 1973). Many biochemical and physiological processes have

been found to be optimal at or near the thermal preferendum. Such processes include growth rate, assimilation efficiency, learning and memory, appetite, digestion, egestion, maximum sustained speed, active metabolic rate, renal function, endocrine action, reproductive activity, enzyme activity, and others (Dawson 1975, Brett 1971, Beitinger and Fitzpatrick 1979). For example, Licht (1965) found that lizards whose BT was kept at 1-2 C above the preferred temperature range for 10 h/day suffered testicular damage within three weeks, while other males kept within the preferred range suffered no damage.

The question of seasonal or diel variation (in the form of endogenous rhythms) in preferred temperature is still an open one for which no generalizations can yet be made (McCauley and Huggins 1979). Laboratory studies on fishes, amphibians, and reptiles show no consistent trends; some species show significant seasonal or diel differences in preferred temperature, while others show no such variation (see reviews in Hutchison and Maness 1979, McCauley and Huggins 1979). Among the three species of Nerodia, only N. cyclopion showed a seasonal difference in preferred temperature, but the summer mean was lower than spring/fall (Walley and Mushinsky in press). Thus to consider seasonally different preferred temperatures would only increase the difference between eccritic and preferred temperatures, and my basic conclusions would not have been changed. Magnuson and Beitinger (1979) stated that terrestrial lizards and

centrarchid fishes have preferred temperatures that are not subject to photoperiodic or seasonal differences.

The basis for temperature regulation apparently lies at the enzymatic and cellular level. Heinrich (1977, p. 627) discussed the possible causes for selection against enzyme duplication: "If the cell contained several temperature isozymes for each of perhaps thousands of its different enzymes and contractile elements, it necessarily has the burden of molecules that at any given temperature are functionless.... Control of the enzyme's immediate environment (e.g., through body-temperature regulation) thus becomes a means of regulating or controlling high rate metabolic processes." It seems that seasonal or diurnal variation in preferred temperature range would not be favored by natural selection.

Differences in eccritic and preferred temperatures in reptiles (mostly lizards) have been reported by Schall (1977), Parker and Pianka (1975), Licht et al. (1966), Pianka (1971), Vance (1973), Heatwole (1970), DeWitt (1967), and Bowker and Johnson (1980). Various explanations have been given, most of which fit into a cost/benefit or economic theory of thermoregulation (Huey and Slatkin 1976, Hainsworth and Wolf 1978). The physiological benefits of thermoregulation must be considered along with the ecological costs. Reynolds (1979) stated that there may be ecological thermal optima that might differ from physiological optima, and trade-offs may sometimes be necessary. Huey and

Webster (1976) estimated the ecological cost in lizard thermoregulation as the distance between escape cover and available sunlight for basking; lizards would not bask if the distance was too far to escape predation.

What ecological factors might be inflating the cost of thermoregulation for Nerodia rhombifera and N. cyclopion? It is possible that N. cyclopion uses the water microhabitat for concealment from predators or foraging for prey even when the water temperature is supraoptimal. Fish have been known to enter waters whose temperatures approached lethal levels to feed for short periods of time (Neill and Magnuson 1974, Engel and Magnuson 1971). DeWitt (1967) suggested that desert iguanas (Dipsosaurus) were forced to allow BT to rise above optimal levels during midday activity due to the unavailability of air temperatures low enough to allow behavioral thermoregulation (shuttling between sun and shade). The alternative to high BT would be a midday period of subterranean inactivity. It is unlikely, however, that unavailability of suitable ambient temperatures was a factor for N. cyclopion; the low TMO values indicate other environmental temperatures in the preferred range.

The ecological costs of thermoregulation in Nerodia rhombifera and N. cyclopion could ultimately be associated with competition. Magnuson et al. (1979) viewed temperature as an ecological resource for which species may be in competition, in the same way as for food and space resources. They found that fish species that have similar thermal

niches (preferred temperature range) when put together in the same tank will shift thermal preference so that each species occupies a different thermal space. A tropical lizard, Anolis oculatus, exhibits a broader thermal niche in the absence of competitors than it does on islands where sympatric congeners are present (Ruibal and Philibosean 1970). Competitive interactions were apparently of little importance in thermal niche positions of Thamnophis radix and T. sirtalis in Manitoba (Hart 1979). The author suggested that physical factors were more important than biotic ones to northern ectotherms enduring a harsh continental climate.

In Louisiana, competitive interactions may be more important in a six-species water snake guild. The three species studied here comprise 86% of the individual water snakes encountered (Mushinsky et al. 1980). A high degree of niche overlap exists between Nerodia cyclopion and N. rhombifera along the food and space axes, while N. fasciata has little overlap with these two species (Mushinsky and Hebrard 1977a, Hebrard and Mushinksy 1978, Kofron 1978). N. cyclopion and N. rhombifera have the narrowest food niches; both are almost completely piscivorous and prefer sparsely vegegetated gently sloping shorelines. Nerodia fasciata seems to be more of a generalist; it feeds on both fish and anurans (this species has the broadest food niche) and shows no habitat preference. When the time axis is considered

N. rhombifera and N. cyclopion have asynchronous daily and seasonal activity periods (Mushinsky and Hebrard 1977b), and Mushinsky et al. (1980) suggested that partitioning of the thermal resource to reduce interference competition is the basis for such asynchrony.

The cost of thermoregulation in Nerodia cyclopion and N. rhombifera may be high due to competition. Consequently, both species had eccritic temperatures that were different from the preferred and in opposite directions (N. cyclopion higher, N. rhombifera lower). Nerodia fasciata, which has relatively little competitive interaction with its two congeners, was able to capitalize on the low cost and high benefits of thermoregulation. Thus it had the highest degree of thermal microhabitat optimization and had an eccritic temperature that exactly equaled its preferred temperature. A fourth congener, N. erythrogaster, is present in relatively small numbers on the study area and is most abundant at night and only during the warmer months. Mushinsky et al. (1980) stated that the potential for niche overlap between N. erythrogaster and sympatric congeners was minimal because of its specialized diet on toads.

Seasonal patterns seem to indicate that Nerodia cyclopion reaches peak activity early in the year, and N. rhombifera later. Nerodia cyclopion has its highest behavioral thermoregulation in spring/fall and winter with the lowest in summer, whereas N. rhombifera shows high thermoregulation

in spring/fall and summer and has its lowest in winter. I made no attempt to distinguish between "active" and "inactive" snakes and was able to census an individual in either state. Mushinsky et al. (1980), using a visual search method, could only census "active" individuals. They found interspecific differences in activity. In spring/fall N. cyclopion and N. fasciata were predominantly diurnal and arboreal while N. rhombifera was more nocturnal and aquatic. In summer all became nocturnally active, but N. rhombifera and N. fasciata were arboreal and N. cyclopion was aquatic. These findings are congruous with those reported here. Air was the most thermally optimal microhabitat in the day in spring/fall, and at night in summer. So the optimum thermal space was occupied by N. cyclopion in spring/fall and by its presumed competitor, N. rhombifera, in summer. Nerodia fasciata which is reported to have less niche overlap with sympatric congeners, used the optimum microhabitat in spring/fall and summer.

Porter and Tracy (1974) estimated that the food biomass needed for reproduction in Thamnophis is about an order of magnitude greater than that needed for maintenance. Their study, as well as other studies on the effects of temperature on reproductive functions (Licht 1965, Vinegar 1974, Osgood 1970, Weil and Aldridge 1979), suggest that thermoregulation may be more critical during times of reproductive activity so that the body will function at optimal efficiency. Nerodia cyclopion and N. rhombifera may be

partitioning their respective reproductive peaks. In addition to the asynchronous thermoregulatory/activity peaks mentioned above, these species show different feeding, reproductive, and abundance peaks. Hebrard and Mushinsky (unpublished data) found that the peak number of gravid individuals of N. cyclopion were taken in May and June, whereas N. rhombifera showed peak gravidity in July and August. Nerodia cyclopion reached an early feeding peak in April, showed a decrease through mid-summer, and had a second peak in late summer/early fall. Nerodia rhombifera had a relatively constant percentage of individuals feeding, but showed a gradual increase from its low point in April to its peak in August. Relative abundance on the study area followed the same trend: N. cyclopion reached peak abundance in May and June and N. rhombifera in July and August.

It seems that Nerodia cyclopion optimizes thermoregulatory processes in the cooler months to enhance early reproduction and spends the warmer months in supraoptimal temperatures. The snakes remain in the water during these months and keep body functions at less than optimal efficiency levels, which are suitable for simple maintenance. Nerodia rhombifera remains cool in the early spring while N. cyclopion is active and the former species does not expend much energy on thermoregulation, then peaks a month or so later than N. cyclopion when N. rhombifera raises its body functions to the efficiency levels necessary for reproduction.

The seasonal differences between species also appear in the land/water relationships. In spring/fall, Nerodia rhombifera was found in open water while N. cyclopion and N. fasciata were at the land/water interface; in summer, all species were usually at the shoreline. Hebrard and Mushinsky (1978) found that most activity was concentrated within one meter of the shoreline, where most feeding takes place. That N. rhombifera remains in open water in spring/fall may indicate a low degree of early feeding in this species. The tendency of aquatic N. rhombifera to frequent deeper water is reflected in its diet. This species generally takes larger fish than do the others and has been known to eat bottom dwellers such as Ictalurus (Mushinsky and Hebrard 1977b).

Nerodia cyclopion and N. rhombifera showed different responses to changing water levels: N. rhombifera was found in open water when water levels were high and on dry land when the levels were low, which indicates that this species does not move to water during dry periods. Nerodia cyclopion was found in deeper water during low water levels than during high water. They probably moved to the deeper, more permanent bodies of water (canals, bayous, etc.) during low water levels and frequented the shallower floodwaters of the backswamps during high water.

The differences in land/water relations may also be indicative of concealment preferences. Nerodia rhombifera

prefers an underground retreat, whereas N. cyclopion prefers an aquatic one, as reflected by their microhabitat frequencies. That N. fasciata was found in the air microhabitat more than the others may be related to the anuran element of its diet (Mushinsky and Hebrard 1977b, Kofron 1978). Mushinsky et al. (1980) also found N. fasciata to be the most arboreal and N. cyclopion the most aquatic species. The use of the underground microhabitat in Nerodia is not well known because of census difficulties. Kofron (1978), Carpenter (1953), and Horton Hobbs (Mike Kearny, personal communication) reported the use of crayfish burrows by snakes. In addition to finding snakes in crayfish burrows, I found them buried in soft mud, not always covered with water, and situated beneath overhangs on the edge of waterways.

Change in distance from the land/water interface and water level between observations did not account for a significant amount of variation in movement rates. Movements to or from (perpendicular to) the shoreline during water level fluctuations were offset by other movements (parallel to the shoreline) during times of constant water levels.

My finding that snakes had a greater movement rate in open water than on dry land indicates the use of water as the primary medium for travel. Schmidt-Nielson (1972) calculated that swimming requires less energy per kilometer of travel than does terrestrial locomotion. Nerodia rhombifera does not seem to move toward inundated areas during low water levels as do the other two speceis. Hebrard and

Mushinsky (unpublished data) found that N. fasciata and N. cyclopion increased in abundance along Bayou Braud and Alligator Bayou during low water periods, but that abundance of N. rhombifera was not correlated with water levels.

It is noteworthy that movement rate was not correlated with temperature. The positive correlation between photoperiod and movement indicates that an annual activity cycle does exist. This cycle seems to be based on the more predictable stimulus rather than temperature, which fluctuated erratically during the study.

Analysis of movement indicated considerable variation. Other studies on snake movements found many small movements and a few that covered greater distances (positively skewed distribution). Recapture studies that reported such a pattern are those by Stickel and Cope (1947), Hebrard and Mushinsky (unpublished data), Fitch and Shirer (1971), and Fraker (1970). Such a pattern could be indicative of spatio-temporal variation in food supply where the animal stays in a certain area until prey items become scarce, then moves to find a new feeding area. Hainsworth and Wolf (1979) stated that most consumer organisms move to obtain food.

Some individuals exhibited a high degree of familiarity with certain parts of their home ranges. Fraker (1970), Hirth (1966), and Landreth (1973) found that displaced snakes showed homing behavior. Freedman and Catling (1979) reported that more than 50% of marked individuals were recaptured within 50 m of the initial capture point.

Newcomer et al. (1974) found that Nerodia sipedon and Regina septemvittata had the ability for celestial navigation by sun-compass orientation.

The home ranges reported here ($\bar{x}$=5.69 ha) are larger than those reported for water snakes in other studies. Fraker (1970) studied Nerodia sipedon in a fish hatchery, and found the home range "small", usually one pond (no area given). Fitch and Shirer (1971) reported that N. sipedon was very sedentary and stayed within a 35 m area for up to 35 days. Preston (1970) found that N. rhombifera moved a mean distance of 194 m, which, if taken as the radius of a circle, is a home range of 2.96 ha. Most of these studies were in pond habitats surrounded by dry land, and it may be that snakes move over a wider area in a swamp situation.

Turner et al. (1966) reported that home range size in lizards is a function of body weight, such that $A=171.4W^{0.95}$ where A=home range area (m^2) and W=body weight (g). They based this equation on home range sizes in the literature from lizards whose body weights ranged from 1.2 to 210.0 g. Although the individuals in my study did not show a significant correlation between body weight and home range size, the above equation fits my results. When 391 g ($\bar{x}$ weight) is substituted for W, the predicted home range area is 49,605 m^2 or 4.96 ha. This figure lies between my polygon estimate (5.96 ha) and ellipse estimate (3.16 ha). The theory is that a large animal will require more food for maintainance energy and thus will have to travel greater

distances to obtain prey (McNab 1963, Harestad and Bunnell 1979). The distribution of prey species must also be considered. Water level fluctuations contribute to prey distribution, since the prey species of most water snakes are aquatic. Water level changes, then, may influence movements from the standpoint of prey distribution, as well as concealment.

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APPENDIX

Appendix 1. Microhabitat prediction model, written in the language of SAS (Barr et al. 1979.).

```
IF SP='RHO' THEN MINPT=23.54;
IF SP='RHO' THEN MAXPT=31.04;
IF SP='CYC' THEN MINPT=21.90;
IF SP='CYC' THEN MAXPT=28.42;
IF SP='FAS' THEN MINPT=23.64;
IF SP='FAS' THEN MAXPT=30.60;
IF MEDIUM ='AIR' THEN AIRSUBT=SUBTEMP;
PA=(MINPT LE AIRTEMP LE MAXPT) OR
(MINPT LE SUNTEMP LE MAXPT) OR (MINPT LE AIRSUBT LE MAXPT);
PW=(MINPT LE WATSURF LE MAXPT) OR
(MINPT LE WATDEEP LE MAXPT);
PU=(MINPT LE GRDTEMP LE MAXPT);
TP=PA+PW+PU;  PRDM='    ';
IF TP=0 THEN LINK ZERO;
IF TP=1 THEN LINK ONE;
IF PRDM NE ' ' THEN REG=(PRDM=MEDIUM);
IF TP=3 THEN REG=1;
IF TP=2 THEN REG=(PA=0 AND MEDIUM NE 'AIR') OR
(PW=0 AND MEDIUM NE 'WAT') OR (PU=0 AND MEDIUM NE 'UNG');
RETURN;
ZERO:
IF AIRTEMP LT MPT AND SUNTEMP GE MINPT THEN PRDM='AIR';
IF PRDM=' ' THEN LINK NOSUN;
RETURN;
```

(continued on next page)

Appendix 1 (continued).

```
NOSUN:
IF MEDTEMP LT MINPT THEN PTEMP=MAX(AIRTEMP, AIRSUBT, WATSURF,
WATDEEP, SUNTEMP, GRDTEMP);
IF MEDTEMP GT MAXPT THEN PTEMP=MIN(AIRTEMP, WATSURF, AIRSUBT,
WATDEEP, GRDTEMP);
IF MEDTEMP=. THEN PTEMP=.
IF PTEMP=AIRTEMP OR PTEMP=SUNTEMP OR PTEMP=AIRSUBT THEN
PRDM='AIR';
IF PTEMP=GRDTEMP THEN PRDM='UNG';
IF PTEMP=WATSURF OR PTEMP=WATDEEP THEN PRDM='WAT';
IF PTEMP=. THEN PRDM='NONE';
RETURN;
ONE:
IF PA=1 THEN PRDM='AIR';
IF PW=1 THEN PRDM='WAT';
IF PU=1 THEN PRDM='UNG';
RETURN;
```

VITA

Thomas Claud Michot

Candidate for the Degree of

Doctor of Philosophy

Dissertation: Thermal and Spatial Ecology of Three Species of Water Snakes (Nerodia) in a Louisiana Swamp.

Major Field: Vertebrate Zoology

Minor Field: Wildlife Management

Biographical Information:

Personal Data: Born at Lafayette, Louisiana, September 30, 1950, son of Louis J. and Patricia S. Michot; married Katharine A. Meleton September 7, 1974; two sons, Andre' Claud and Louis Pierce.

Education: Attended elementary school in Lafayette, Louisiana, and Annandale, Virginia; was graduated from Cathedral-Carmel High School, Lafayette, Louisiana, in 1968; received Bachelor of Science degree from University of Southwestern Louisiana in 1972, with a major in Zoology, Wildlife Management option; attended University of Minnesota, Lake Itasca Biology Station, in 1973; received a Master of Science degree from Utah State University in 1976, with a major in Wildlife Science; completed requirements for Doctor of Philosophy degree at Louisiana State University in 1981.

Experience: Biologist, US Fish and Wildlife Service, 1981 to present; Teaching Assistant and Research Assistant, Louisiana State University, 1976-1980; Research Assistant, Utah Cooperative Wildlife Research Unit, 1974-1976; Environmental Education Coordinator, Louisiana State Arts Council, 1972-1973.

EXAMINATION AND THESIS REPORT

Candidate: Thomas Claud Michot

Major Field: Zoology

Title of Thesis: Thermal and spatial ecology of three species of water snakes (Nerodia) in a Louisiana swamp.

Approved:

W J Hamman
Major Professor and Chairman

Séan McGlynn
Dean of the Graduate School

EXAMINING COMMITTEE:

Henry R. Mushinsky

Douglas A. Rossman

J Michael Fitzsimons

John Dennemann

Date of Examination:

October 16, 1981